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ORIGINAL ARTICLE

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The marine macroalgae of Helgoland (North Sea): an annotated list of records between 1845 and 1999

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Abstract The earliest known records of marine macroalgae from Helgoland (German Bight, North Sea) date from the mid-19th century. Since then, 274 marine macroalgal species have been reported: 77 species of Chlorophycota, 100 species of Phaeophycota and 97 species of Rhodophycota. Additionally 11 species were only recorded as drift and 51 species as doubtful for Helgoland. The remains of the herbarium of Paul Kuckuck, the first curator for botany at the Helgoland Biological Station between 1892 and 1914, are still located there and consist of 173 macroalgal species from Helgoland. On comparing this 100-year-old herbarium and other old sources with recent macroalgal records, it became clear that changes in species composition have occurred. After World War II, several species such as *Arthrocladia villosa*, *Corynophlaea crispa*, *Cutleria multifida*, *Eudesme virescens*, *Mesogloia vermiculata*, *Sporochnus pedunculatus*, *Antithamnion cruciatum*, *Apoglossum ruscifolium*, *Chondria dasyphylla*, *Helminthothra divaricata*, *Jania rubens* and *Osmundea ramosissima* were not found again. Other species such as *Dictyota dichotoma*, *Leathesia difformis*, *Stictyosiphon soriferus*, *Helminthocladia calvadosii* and *Scinaia furcellata* became very rare. Significantly, perhaps, most of these species have a heteromorphic life history with the appearance of the macroscopic phase restricted to (spring and) summer. Many new species of green algae were recorded for Helgoland after 1959, due to new substrata and the research activities of Peter Kornmann, curator for botany after 1959, and Paul-Heinz Sahling his technical assistant. Introductions of species during the considered time period were: *Bonne-*

maisonia hamifera, *Codium fragile*, *Mastocarpus stellatus* and *Sargassum muticum*. Type material of the following species is located at the Marine Biological Station at Helgoland: *Mikrosyphar porphyrae*, *Porphyra insolita* and *Ulva tenera*.

Keywords Phycology · Macroalgae · Helgoland · Checklist · Biodiversity Change

Introduction

Phycological research on Helgoland was started in the mid-19th century by amateur phycologists and was continued by professional scientists. Towards the end of the 19th century, Johannes Reinke (1849–1931) was the leading phycologist in Germany. He promoted Paul Kuckuck (1866–1918) to become the first curator of botany at the Marine Station on Helgoland (Biologische Anstalt Helgoland) in 1892 (Mollenhauer and Lüning 1988). Wollny (1881) compiled the first checklist of marine macroalgae for Helgoland based on own collections during six consecutive summers and earlier published records, probably mostly from Kützing's work (Kützing 1845, 1849). But Kuckuck initiated the first thorough description of the Helgoland marine flora, which was continued by Wilhelm Nienburg (1882–1932) and Otto Christian Schmidt (1900–1951) from the 1920s to 1930s, followed by Peter Kornmann (1907–1993) and his technical assistant Paul-Heinz Sahling (born 1911) after 1959. The more conspicuous part of the marine flora of the island was described in a textbook and in two additions to it by Kornmann and Sahling (1977, 1983, 1994). Many more publications by these and other authors exist, dealing with the rare or microscopic benthic algae of Helgoland.

The aim of the present study was to compile an annotated list of the marine benthic algae described for Helgoland, including all publications describing of the rare or doubtful species, in an attempt to make the scattered literature available and to present a qualitative insight in-

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to the floristic changes that have taken place over the last century and that have already been partly described by Kornmann and Sahling (1994). Additionally, the taxa presented in the remains of Kuckuck's herbarium on Helgoland and in the herbarium of Kornmann and Sahling are also listed.

Materials and methods

The list is based on the parts of Paul Kuckuck's herbarium that survived the 1939–1945 war, on the Helgoland herbarium of Peter Kornmann and Paul-Heinz Sahling, which they started in the late 1950s and which is still located on Helgoland, and on all literature dealing with macroalgal species at Helgoland that have come to the knowledge of the authors from Kützing (1845) onwards. The main part of Kuckuck's herbarium was destroyed and a complete list of his collections no longer exists (see Mollenhauer and Lüning 1988). The publication list of Peter Kornmann and Paul-Heinz Sahling was examined in full, but only those titles that deal with Helgoland species have been included here. A complete publication list of these authors is available in Lüning (1994). The presence of Type material that is still available at the Helgoland Marine Station is indicated in the list. A running herbarium number for Kuckuck's as well as for Kornmann's and Sahling's herbarium sheets has never been available until now. The huge collection of permanent microscope slides and of formalin-preserved material belonging to Kornmann and Sahling was taken into consideration as additional information if no herbarium sheets were present for a specific taxon. It should be mentioned here that there is also a large archive of photographic material of the work of Kornmann and Sahling, which is still available. Species names and authorities generally follow Guiry (2000). Abbreviations and

sources used for the compilation of the list are given in Table 1. The abbreviations of author names follow Brummitt and Powell (1992). In Table 2, only those synonyms for algae that were used in the cited references are listed, in order to facilitate the use of old sources. The authorities for species names in old publications were often missing, incomplete or false; and thus Guiry (2000) was also followed here. Species that are discussed in more detail are marked with asterisks in Table 2. Old species names used in Kützing (1845) and Wollny (1881) that could not be correlated with current taxa were omitted.

Information about macroalgal species from Helgoland that can be found in the herbaria of Hamburg, Kiel and Berlin, as well as in other European and non-European herbaria, was not considered.

If the geographical distribution of species was considered, only areas adjacent to Helgoland (namely NE England, the Netherlands, Denmark and Norway) were taken into account in order to give information about the possibility of finding the species currently on Helgoland.

Results

The 274 macroalgal species reported from Helgoland are listed in Table 2, including 77 species of Chlorophycota, 100 species of Phaeophycota and 97 species of Rhodophycota. Additionally 11 drift species were recorded. A total of 214 species was recorded for the time period 1845–1935 as well as for 1959–1998. Nevertheless, a change in recorded species is evident when comparing these two periods. Of the algae found after 1959, 68 species belong to the Chlorophycota, 65 to the Phaeophycota and 81 to the Rhodophycota, whereas from 1860 to the 1930s about 40% fewer species of Chlorophycota were found (41 versus 68), a similar number of Rhodophycota species (81 versus 84), but 27% more species of Phaeophycota (89 versus 65), compared with the later period.

Table 2 also presents a list of species with doubtful records for Helgoland that comprises 51 species in total: 7 Chlorophycota, 11 Phaeophycota and 33 Rhodophycota. All species that were mentioned only by one or two authors without any reference regarding the origin of the material (herbarium reference, collector, drift or not) or a detailed description (including drawings or herbarium specimens) were gathered together under this heading. In many cases these species show a distribution in which Helgoland would have been the northernmost extension (Guiry 2000), making the record even more doubtful. Furthermore this list includes many taxa that have undergone considerable taxonomical and nomenclatural revision (e.g. *Cladophora*, *Enteromorpha*, *Ectocarpus*, *Sphacelaria*, *Acrochaetium*, *Laurencia*, *Osmundea* and *Polysiphonia*) so that former misidentifications cannot be ruled out.

Chlorophycota

Acrosiphonia spp

For the separation of species in the *Acrosiphonia-Spongomorpha* complex we follow the school of thought

Table 1 Abbreviations and sources for compilation of Table 2. Year of publication is only indicated if not mentioned in Table 2

Abbreviation	Author	Source
B	Bartsch	Personal observation
BP	Burkhardt and Peters	1998
C	Cohn	1865
D	Damman	
EP	Ellertsdóttir and Peters	1997
H	Harms	1993
Hal	Hallier	1863
Hau	Hauck	1885
Herb.Gä.	Herbarium Gätje	Mid-19th century
Herb.Ku.	Herbarium Kuckuck	1892–1912
Hey	Heydrich	1900
K	Kornmann	
KS	Kornmann and Sahling	1977, 1983, 1994
Ku	Kuckuck	
Kuhl	Kuhlenkamp	Personal observation
Kütz	Kützing	1845
Lü	Lüning	1970
Leu	Leukart	1989, 1992
N	Nienburg	
P	Peters	
PHR	Prud'homme van Reine	
PE	Peters and Ellertsdóttir	1996
Pr	Pringsheim	1862
R	Reinke	
S	Schmidt	
Sch	Schiller	1928
T	Tittley	1982
vdH	van den Hoek	
W	Wollny	
Z	Zimmermann	1923

Table 2 Checklist of marine macroalgae from Helgoland. *Italics* indicate synonyms used in references, *asterisks* indicate taxa which are commented upon in the annotations, *No.* Number of herbarium sheets present in the herbarium Kuckuck, *X* present in

respective herbarium. *Cross-hatched to the left* indicates taxa not recorded 1845–1935; *cross-hatched to the right* indicates taxa not recorded 1959–1998. For abbreviations of references see Table 1

CHLOROPHYCOTA:	Herb. Ku	No.	1845-1935	1959-1998	Herb. KS
<i>Acrochaete repens</i> Pringsh.			W1881, Ku1894b		
<i>Acrochaete parasitica</i> Oltm.					
<i>Acrochaete wittrockii</i> (Wille) R. Nielsen				KS	
<i>Phaeophila wittrockii</i> (Wille) R. Nielsen					
* <i>Acrosiphonia arcta</i> (Dillwyn) J. Agardh				KS, K1962b, K1964b, H, B, Lü	X
* <i>Acrosiphonia centralis</i> (Lyngb.) Kjellm.				KS, K1962b, H, B	X
* <i>Acrosiphonia sonderi</i> (Kütz.) Kornmann	X		Kütz, W1881, Hau	KS, K1962b, H, B	X
<i>Cladophora sonderi</i> Kütz.		1			
? <i>Cladophora spongomorpha sonderi</i>					
<i>Blastophysa rhizopus</i> Reinke			Ku1897a		
* <i>Blidingia chadefaudii</i> (Feldmann) Bliding				KS 1978	X
* <i>Blidingia marginata</i> (J. Agardh) P.J.L. Dang. ex Bliding	X		W1881	KS, KS1978, H, B	X
<i>Enteromorpha marginata</i> J. Agardh		1			
* <i>Blidingia minima</i> (Nägeli ex Kütz.) Kylin			W1881	KS, KS1978, H, B	X
<i>Enteromorpha micrococca</i> Kütz.					
<i>Enteromorpha minima</i> Nägeli ex Kütz.					
* <i>Blidingia subsalsa</i> (Kjellm.) Kornmann et Sahling				KS1978	X
* <i>Bolbocoleon piliferum</i> Pringsh.	X	2		EP	
* <i>Bryopsis hypnoides</i> J. V. Lamour.			S1935	KS, Lü, H, B	
* <i>Bryopsis lyngbyei</i> Hornem.	X		W1881, Ku1894b	KS, KS1976, H, B	X
<i>Bryopsis plumosa</i> (Huds.) C. Agardh		3			
<i>Capsosiphon fulvescens</i> (C. Agardh) Setch. et N. L. Gardner				KS, H	X
* <i>Chaetomorpha ligustica</i> (Kütz.) Kütz.				KS, K1972, Lü, H, B	X
<i>Chaetomorpha tortuosa</i> Kütz.					
<i>Chaetomorpha linum</i> (O. F. Müller) Kütz.	X		Hal, W1881, N1925	KS, K1972, H, B	X
<i>Chaetomorpha aerea</i> (Dillwyn) Kütz.		3			
<i>Chaetomorpha crassa</i> (C. Agardh) Kütz.					
<i>Chaetomorpha melagonium</i> (F. Weber et D. Mohr) Kütz.	X	3	Hal, W1881	KS, K1972, Lü, H, B	X
* <i>Cladophora albida</i> (Nees) Kütz.	X	1		KS, H	X
* <i>Cladophora dalmatica</i> Kütz.				KS, vdH1963	X
* <i>Cladophora laetevirens</i> (Dillwyn) Kütz.			vdH1963	KS, vdH1963	
* <i>Cladophora lehmanniana</i> (Lindenb.) Kütz.	X	10	Kütz, W1881, Hau, N1925	KS, vdH1963	X
<i>Cladophora arcta</i>		3			
<i>Cladophora macallana</i> Harv.					
<i>Cladophora utriculosa</i> f. <i>lehmanniana</i>					
* <i>Cladophora rupestris</i> (L.) Kütz.	X	12	W1881, Ku1905, N1925	KS, Lü, H, B	X
<i>Cladophora lyngbyana</i>					
<i>Cladophora rupestris nuda</i> (Harv.) Holmes et Batters					
* <i>Cladophora sericea</i> (Huds.) Kütz.	X	13		KS, H, B	X
* <i>Cladophora vagabunda</i> (L.) C. Hoek				KS, vdH1963	X

which distinguishes the genera on the basis of nuclear number (*Acrosiphonia*: multinucleate and *Spongomorpha*: uninucleate cells). For a detailed discussion about the work of Kornmann and Jonsson in this species complex see Silva et al. (1996) (App. II, 931–934). In the Kuckuck herbarium there is material under the name of *A. setacea* Kjellmann that has not yet been verified.

Blidingia spp.

Several *Blidingia* species became prominent members of the flora after the establishment of artificial substrata at Helgoland. In the 19th century some species were recorded by Wollny (1881) and are present in the Kuckuck herbarium, but were probably not a conspicuous part of

Table 2 (continued)

CHLOROPHYCOTA:	Herb. Ku	No.	1845-1935	1959-1998	Herb. KS
* <i>Codium fragile</i> (Sur.) Hariot			S1935	KS, Lü, H, B	X
* <i>Derbesia marina</i> (Lyngb.) Solier	X	2	R1888, Ku1894b, Ku1905, N1925	KS, Lü	X
<i>Halicystis ovalis</i> (Lyngb.) Aresch.					
<i>Valonia ovalis</i> (Lyngb.) Agardh		1			
* <i>Enteromorpha clathrata</i> (Roth) Grev.			W1881, N1925	KS	X
? <i>Enteromorpha lingulata</i>					
* <i>Enteromorpha compressa</i> (L.) Nees	X	35	W1881, Ku1894b, N1925	KS, H, B	X
* <i>Enteromorpha flexuosa</i> (Wulfen) J. Agardh				KS	X
* <i>Enteromorpha intestinalis</i> (L.) Nees	X	1	W1881	KS, H	X
* <i>Enteromorpha linza</i> (L.) J. Agardh	X	20	Ku1894b, N1925	KS, H, B	X
* <i>Enteromorpha muscoides</i> (Clemente) Cremades	X		W1881		
<i>Enteromorpha crinita</i> Nees		2			
<i>Enteromorpha ramulosa</i> (J. E. Smith) Carmich.					
* <i>Enteromorpha prolifera</i> (O. F. Müll.) J. Agardh				KS, H, B	X
* <i>Enteromorpha torta</i> (Mert.) Reinbold				KS, B	X
<i>Entocladia flustrae</i> (Reinke) Taylor	X				
<i>Epicladia flustrae</i> Reinke		1			
* <i>Entocladia viridis</i> Reinke			S1935		
<i>Endoderma viride</i> (Reinke) Lagerh.					
* <i>Gomontia polyrhiza</i> (Lagerh.) Bornet et Flahault	X	1	S1935		
* <i>Halochlorococcum dilatatum</i> Kornmann et Sahling				KS	
<i>Halochlorococcum marinum</i> P. L. J. Dang.				KS	
<i>Halochlorococcum moorei</i> (N. L. Gardner) Kornmann et Sahling			Z, S1935	KS	
<i>Chlorochytrium willei</i> Printz					
<i>Chlorocystis cohnii</i> (Wright) E. G. Reinhard					X
* <i>Halochlorococcum operculatum</i> Kornmann et Sahling				KS	
<i>Kornmannia leptoderma</i> (Kjellm.) Bliding			S1938a	KS, KS1962b	
<i>Monostroma helgolandicum</i> Schmidt					
<i>Monostroma leptodermum</i> Kjellm.					
<i>Monostroma arcticum</i> Wittr.				KS1962b, KS, B	X
<i>Monostroma grevillei</i> (Thur.) Wittr.	X	4	Ku1905	K1962a, KS1962b, KS, H, B	X
<i>Monostroma oxyspermum</i> (Kütz.) Doty				KS	
<i>Ulvaria oxysperma sensu</i> Kornmann et Sahling 1994					
<i>Ochlochaete hysterix</i> Thwaites ex Harv.	X				
<i>Ochlochaete lentiformis</i> Huber		1			
<i>Ostreobium quekettii</i> Bornet et Flahault				KS1980b	
<i>Percursaria percurta</i> (C. Agardh) Rosenv.				KS, B	X
<i>Phaeophila tenuis</i> (Kyllin) R. Nielsen				KS	
<i>Planophila microcystis</i> (P. L. J. Dang.) Kornmann				KS	
<i>Prasiola calophylla</i> (Carmich. ex Grev.) Kütz.				KS, KS1974	
<i>Prasiola furfuracea</i> (Mert. ex Hornem.) Kütz.				KS1974	X
<i>Prasiola stipitata</i> Suhr ex Jess.				KS, H, B	X
<i>Pringsheimiella scutata</i> (Reinke) Höhn. ex Marchew.	X	2		KS	
<i>Protomonostroma undulatum</i> (Wittr.) K. L. Vinogr.				KS1962b, KS, H, B	X
<i>Monostroma undulatum</i> Wittr.					
<i>Pseudodendroclonium dynamenae</i> R. Nielsen				KS	
<i>Rhizoclonium kochianum</i> Kütz.			S1935	KS, H	
<i>Rhizoclonium riparium</i> (Roth) Kütz. ex Harv.	X	1		KS, H, B	X
* <i>Rosenvingiella constricta</i> (Setch. et N. L. Gardner) P. C. Silva				KS, KS1974	X
<i>Rosenvingiella polyrhiza</i> (Rosenv.) P. C. Silva				KS, KS1974	X
* <i>Spongomorpha aeruginosa</i> (L.) C. Hoek	X		Ku1894b, Ku1897a	K1961a, K1964c, KS, H, Leu	
<i>Cladophora lanosa</i> Harv.		9			

Table 2 (continued)

CHLOROPHYCOTA:	Herb. Ku	No.	1845-1935	1959-1998	Herb. KS
<i>Codiolum petrocelidis</i> Kuck.		2			
<i>Spongomorpha lanosa</i> (Roth) Kütz.					X
<i>Stromatella monostromatica</i> (P. J. L. Dang.) Kornmann et Sahling				KS, Leu	
<i>Stromatella papillosa</i> (P. A. Dang.) Kornmann et Sahling				KS, Leu	
<i>Sykidion droebakense</i> Wille			S1938b		
<i>Syncoryne reinkei</i> R. Nielsen et P. M. Pedersen				KS	
* <i>Ulothrix flacca</i> (Dillwyn) Thur. in Le Jolis	X	4	W1881, Ku1894b, N1925		X
? <i>Ulothrix collabens</i> (Agardh) Thur.		1			
<i>Hormotrichum fasciculare</i> Kütz.					
<i>Hormotrichum vermiculare</i> Kütz.		2			
* <i>Ulothrix implexa</i> (Kütz.) Kütz.			W1881	K1964a	
<i>Ulothrix acrorhiza</i> Kornmann					
<i>Ulothrix subflaccida</i> Wille					
* <i>Ulothrix speciosa</i> (Carmich. ex Harv. in Hooker) Kütz.				K1961c, K1964a, KS	X
<i>Ulothrix flexuosa</i> Kornmann					slides
<i>Urospora speciosa</i> (Carmich.) Leblond ex Hamel					
* <i>Ulva curvata</i> (Kütz.) De Toni			W1881, R1891a, Ku1894b, Sch, S1935, S1938a	KS	X
<i>Ulva kuckuckiana</i> Schmidt					
<i>Phycoseris curvata</i> Kütz.					
* <i>Ulva lactuca</i> L.	X	4	W1881, N1925	KS, H, B	X
<i>Ulva latissima</i>		5			
* <i>Ulva pseudocurvata</i> Koeman et C. Hoek				KS	X
* <i>Ulva tenera</i> Kornmann et Sahling				KS	Type
<i>Ulvella lens</i> P. Crouan et H. Crouan				KS	
<i>Uronema curvata</i> Printz				KS	
<i>Urospora curvata</i> (Printz) Kornmann					
<i>Urospora neglecta</i> (Kornmann) Lokhorst et Trask	X		W1886, Ku1897a	KS, K1961b, K1966, H, B	
<i>Hormiscia neglecta</i> Kornmann					
<i>Codiolum gregarium</i> A. Braun		1			
<i>Urospora penicilliformis</i> (Roth) Aresch.	X	9	Ku1894b, N1925	K1961c, K1966, KS, H	X
<i>Urospora bangioides</i> (Harv.) Holmes et Batters					X
<i>Hormiscia penicilliformis</i> (Roth) Aresch.					
<i>Hormiscia penicilliformis</i> (Roth) Fries					
<i>Urospora wormskioldii</i> (Mert. ex Hornem.) Rosenv.				K1961c, KS	X
? <i>Codiolum wormskioldii</i> (Mert.) Kornmann					
Doubtful records:					
<i>Chaetomorpha fibrosa</i> Kütz.			W1881		
* <i>Cladophora battersii</i> C. Hoek			W1881		
<i>Cladophora refracta</i> (Roth) Kütz.					
* <i>Cladophora pellucida</i> (Huds.) Kütz.			Kütz		
<i>Cladophora trichotoma</i> (C. Agardh) Kütz.					
<i>Enteromorpha flexuosa</i> subsp. <i>paradoxa</i> (C. Agardh) Bliding			W1881		
<i>Enteromorpha paradoxa</i> (C. Agardh) Kütz.					
* <i>Entonema tenuissimum</i> Reinsch			W1881		
<i>Periplegmaticum ceramii</i> Kütz.			Kütz, W1881		
<i>Ulva lobata</i> (Kütz.) Setch. et N. L. Gardner			W1881		
<i>Phycoseris lobata nana</i> Kütz.					
PHAEOPHYCOTA:					
<i>Acinetospora crinita</i> (Carmich. ex Harvey) Kornmann				KS, B	X

Table 2 (continued)

CHLOROPHYCOTA:	Herb. Ku	No.	1845-1935	1959-1998	Herb. KS
Actinema scutellum Reinsch			W1881		
*Arthrocladia villosa (Huds.) Duby	X	1	W1881, Ku1894b, R1891a		
<i>Arthrocladia septentrionalis</i>					
*Ascophyllum nodosum (L.) Le Jol.	X	8	W1881, R1891a, Ku1905, N1925, S1928	KS, H, B	X
<i>Ozothallia vulgaris</i> Decaisne et Thuret					
*Asperococcus fistulosus (Huds.) Hook.	X		Kütz, W1881, Ku1905, Ku1912		
<i>Asperococcus echinatus</i> (Mert. in Roth) Grev.		8			
<i>Encoelium echinatum</i>					
Botrytella micromora Bory	X		W1881, Hau, Pr, R1891a	KS1984, KS1988, KS	X
<i>Botrytella uvaeformis</i> (Pringsh.) Kornmann et Sahling					
<i>Sorocarpus uvaeformis</i> Pringsh.		7			
<i>Sorocarpus micromorus</i> (Bory) P. C. Silva					
Botrytella reinboldii (Reinke) Kornmann et Sahling			R1892	KS1984, KS1988	
<i>Ectocarpus reinboldii</i> Reinke	X	1			
<i>Sorocarpus reinboldii</i> (Reinke) Kornmann et Sahling					
Botrytella spec.				KS1984, KS1988	
<i>Sorocarpus spec.</i>					
Chilionema foecundum (Strömfelt) Fletcher	X				
<i>Phycocelis foecunda</i> Strömfelt		1			
*Chilionema reptans (P. Crouan et H. Crouan) Sauv.			Ku1953		
Chorda filum (L.) Stackh.	X	6	W1881, R1891a, N1925	KS, H	X
Chordaria flagelliformis (O. F. Müll.) C. Agardh	X	21	Hal, W1881, R1891a, N1925	KS1962c, KS, H, B	X
*Cladostephus spongiosus (Huds.) C. Agardh	X	18	Kütz, Hal, W1881, R1891a, Ku1912, N1925	KS, Lü, H, B	X
<i>Cladostephus densus</i> Kütz.		6			
<i>Cladostephus myriophyllum</i>					
<i>Cladostephus verticillatus</i> C. Agardh					X
*Compsonema saxicolum (Kuck.) Kuck.			Ku1897a, Ku1953		
<i>Myrionema saxicolum</i> Kuck.					
*Corynophlaea crispa (Harv.) Kuck.	X		Ku1897a, Ku1929		
<i>Leathesia concinna</i> Kuck.					
<i>Leathesia crispa</i> Harv.		5			
*Cutleria multifida (Sm.) Grev.	X	11	W1881, R1891a, Ku1894b, Ku1900, N1925		
<i>Aglaozonia parvula</i> (Grev.) Zanardini					
<i>Aglaozonia reptans</i> (P. Crouan et H. Crouan) Kütz.					
*Delamarea attenuata (Kjellm.) Rosenv.	X	2	Ku1894b		
Desmarestia aculeata (L.) J. V. Lamour.	X	25	Hal, W1881, R1891a, Ku1894b, N1925	KS, Lü, H, B	X
Desmarestia viridis (O. F. Müll.) J. V. Lamour.	X	10	Hal, W1881, R1891a, N1925	KS, Lü, H, B	X
Dichosporangium chordariae Wollny	X	1	Ku1954		
<i>Streblonema chordariae</i> (Wollny) Cotton					
*Dictyosiphon foeniculaceus (Huds.) Grev.	X	22	Hal, W1881, Ku1912, N1925, S1928	KS	X
<i>Dictyosiphon hippuroides</i> (Lyngb.) Kütz.	X	3			

Table 2 (continued)

CHLOROPHYCOTA:	Herb. Ku	No.	1845-1935	1959-1998	Herb. KS
*Dictyota dichotoma (Huds.) J. V. Lamour.	X	12	Hal, W1881, C1865, R1891a, Ku1905, N1925	KS, Lü, B	X
Ectocarpus fasciculatus Harv.	X	8	W1881, R1891a, N1925	KS, H, B	X
*Ectocarpus lucifugus Kuck.	X	2	Ku1897b		
Ectocarpus minimus Nägeli	X	1			
Ectocarpus siliculosus (Dillwyn) Lyngb.	X	20	W1881, R1891a, Ku1894b, Ku1897a, Ku1912	KS, H	X
<i>Ectocarpus confervoides</i> (Roth) Le Jol.		4			
<i>Ectocarpus dasycarpus</i> Kuck.		2			
<i>Ectocarpus penicillatus</i> (C. Agardh) Kjellm.					
Elachista fucicola (Velley) Aresch.	X	10	R1891a, N1925	K1962c, KS, H, B	X
*Eudesme virescens (Carmich. ex Berk.) J. Agardh	X		Kütz, Hal, W1881, Ku1929		
<i>Castagnea virescens</i> (Carmich.) Thur.		20			
<i>Mesogloia virescens</i> Carmich. ex Berk.					
*Fucus ceranoides L.				KS	
Fucus serratus L.	X	3	W1881, R1891a, N1925	KS, Lü, H, B	X
Fucus spiralis L.	X		W1881, R1891a, N1925	KS, H, B	X
<i>Fucus platycarpus</i> Thur.		4			
Fucus vesiculosus L.	X	10	Hal, W1881, R1891a, N1925	KS, H, B	X
Halidrys siliquosa (L.) Lyngb.	X	5	Hal, W1881, R1891a, N1925	KS, Lü, H, B	X
Halosiphon tomentosus (Lyngb.) Jaasund	X		W1881, R1891a, N1925	KS, Lü, H, B	X
<i>Chorda tomentosa</i> Lyngb.		15			
Haplospora globosa Kjellm.	X	3	R1891a, N1923	KS	X
*Hecatonema terminale (Kütz.) Kylin			Kütz, W1881, Hau, Ku1897a, Ku1953		
<i>Ectocarpus terminalis</i> Kütz.					
<i>Hecatonema maculans</i> (Collins) Sauv.					
Herponema velutinum (Grev.) J. Agardh	X		W1881, Hau, Ku1956		
<i>Ectocarpus velutinus</i> (Grev.) Kütz.		1			
*Himanthalia elongata (L.) Gray	X		Hal (Drift), W1881, Hau	KS, Kuhl	
<i>Himanthalia lorea</i> (L.) Lyngb.		1			
*Hincksia fuscata (Zanardini) P. C. Silva in P. C. Silva, Menez & Moe	X		Ku1961, K1954	K1954, KS	
<i>Ectocarpus fuscatus</i> Zanardini in Menegh.		4			
<i>Giffordia fuscata</i> (Zanardini) Kuck.					
Hincksia granulosa (Sm.) P. C. Silva in P. C. Silva, Menez & Moe	X		Ku 1912, Ku1961	KS, B	X
<i>Ectocarpus granulatus</i> (Sm.) C. Agardh		18			
<i>Giffordia granulosa</i> (Sm.) Hamel					
Hincksia hincksiae (Harv.) P. C. Silva in P. C. Silva, Menez & Moe				KS	X
Hincksia sandriana (Zanardini) P. C. Silva in P. C. Silva, Menez & Moe				KS	X
*Isthmoplea sphaerophora (Carmich.) Kjellm.	X	5	R1891a, R1892	KS	X
Kuckuckia spinosa (Kütz.) Kuck.			Ku1958		
<i>Ectocarpus criniger</i> Kuck.					
Kuetzingiella holmesii (Batters) Russell	X		Ku1897a	KS, T	
<i>Ectocarpus holmesii</i> Batters		1			
*Kuetzingiella maculans (Kuck.) Kornmann			Ku1897a, Ku1956		
<i>Ectocarpus</i> (?) <i>maculans</i> Kuck.					

Table 2 (continued)

CHLOROPHYCOTA:	Herb. Ku	No.	1845-1935	1959-1998	Herb. KS
Laminaria digitata (Huds.) J. V. Lamour.	X	5	Hal, R1891a, Ku1894b, N1925	KS, Lü, H, B	X
<i>Laminaria flexicaulis</i> Le Jol.					
Laminaria hyperborea (Gunnerus) Foslie			Hal, R1891a, N1925	KS, Lü, H, B	X
<i>Laminaria cloustonii</i> Edmonston					
Laminaria saccharina (L.) J. V. Lamour.	X	35	Kütz, Hal, W1881, R1891a, Ku1894b, N1925	KS, Lü, H, B	X
<i>Laminaria cuneifolia</i> J. Agardh		1			
<i>Ulva latissima</i> L.					
Laminariocolax aecidioides (Rosenv.) Peters	X		Ku1894b	BP	
<i>Phycocelis aecidioides</i> (Rosenv.) Kuck.		6			
Laminariocolax tomentosoides (Farl.) Kylin	X			KS, H, BP	
<i>Ectocarpus tomentosoides</i> Farl.		4			
Laminarionema elsbethiae Kawai et Tokuyama				PE	
*Leathesia difformis (L.) Aresch.	X	8	Hal, W1881, Ku1894b, Ku1905, N1925, S1928, D1930		
<i>Leathesia marina</i> (C. Agardh) J. Agardh					
Leptonematella fasciculata (Reinke) P. C. Silva	X		R1891a	KS, H	
<i>Leptonema fasciculatum</i> Reinke		5			
Litosiphon laminariae (Lyngb.) Harv.				KS1990	
<i>Litosiphon pulsillus</i> (Carmich. ex Hook.) Harv.					
*Mesogloia vermiculata (Sm.) Gray	X	3	Kütz, Hal, W1881, R1891a		
<i>Mesogloia vermicularis</i> C. Agardh					
Microspongium globosum Reinke				KS	X
*Mikrosyphar polysiphoniae Kuck.			Ku1897a, Ku1897b	KS	
Mikrosyphar porphyrae Kuck.	Type	1	Ku1897a, Ku1897b		
Myrionema strangulans Carmich. ex Grev.	X	3	Hal, W1881, R1891a	KS	X
<i>Myrionema maculiforme</i> Kütz.		2			
<i>Myrionema punctiforme</i> Harv.					
Petalonia fascia (O. F. Müll.) Kuntze	X		Kütz, Hal, W1881, R1891a	KS, H, B	X
<i>Phycolapathum cuneatum</i> Kütz.					
<i>Phyllitis fascia</i> (O. F. Müll.) Kütz.		20			
*Petalonia filiformis (Batters) Kuntze	X		Ku1897a		
<i>Phyllitis filiformis</i> Batters		1			
Petalonia zosterifolia (Reinke) Kuntze	X		Ku1894b, Ku1912	KS, H, B	X
<i>Phyllitis zosterifolia</i> Reinke		12			
Petroderma maculiforme (Wollny) Kuck.	X	1	W1881, Ku1897a		
<i>Lithoderma maculiforme</i> Wollny					
*Petrospongium berkeleyi (Grev.) Nägeli ex Kütz.			Hau, W1881		
<i>Leathesia berkeleyi</i> (Grev.) Harv.					
Phaeostroma pustulosum Kuck.	X		Ku1897a		
<i>Phaeostroma aequale</i> (Oltm.) Kuck.		2			
Pilayella littoralis (L.) Kjellm.	X	22	N1925, D1930	KS, H, B, T	X
Pilayella varia Kjellm.				K1990	
<i>Pilayella macrocarpa</i> Foslie					
*Pilinia rimosa Kütz.	X		Ku1897a, Ku1897b	T	
<i>Leptonema lucifugum</i> Kuck.		2			
<i>Waerniella lucifuga</i> (Kuck.) Kylin					
Pogotrichum filiforme Reinke	X	6		KS, H	X
<i>Litosiphon filiformis</i> (Reinke) Batters					
Protectocarpus hecatonemoides Kuck.			Ku1955		
Protectocarpus speciosus (Boergs.) Kuck. ex Kornmann			Ku1955	KS	

Table 2 (continued)

CHLOROPHYCOTA:	Herb. Ku	No.	1845-1935	1959-1998	Herb. KS
<i>Pseudolithoderma extensum</i> (P. Crouan et H. Crouan) S. Lund	X		W1881, W1886, Hau, R1891a, Ku1894b, Ku1912	P1989	
<i>Lithoderma fatiscens</i> Aresch.		4			
<i>Punctaria latifolia</i> Grev.	X	2	Hal, Ku1894b, Ku1905	KS, H	X
<i>Punctaria hiemalis</i> Kylin					
<i>Punctaria plantaginea</i> (Roth) Grev.	X	19	Kütz, Hal, W1881, R1891a, Ku1912	KS, H, B	X
<i>Phycolapathum plantagineum</i> (Roth) Kütz.					
<i>Punctaria tenuissima</i> (C. Agardh) Grev.	X		Hal, W1881		
<i>Desmotrichum undulatum</i> (J. Agardh) Reinke		2			
<i>Diplostromium tenuissimum</i> (C. Agardh) Kütz.					
<i>Ralfsia verrucosa</i> (Aresch.) Aresch.	X	2	W1881, R1891a, Ku1894b	KS, H, T	
* <i>Sargassum muticum</i> (Yendo) Fensholt				KS, H, B	X
* <i>Sauvageaugloia griffithsiana</i> (A. W. Griffiths ex Harv.) Hamel ex Kylin			W1881, Ku1912		
? <i>Castagnea griffithsiana</i> (Grev.) Agardh					
<i>Mesogloia griffithsiana</i> A. W. Griffith ex Harv.					
<i>Scytosiphon lomentaria</i> (Lyngb.) Link	X		Hal, W1881, R1891a, Ku1912, D1930	KS, H, B	X
<i>Chorda lomentaria</i> Lyngb.					
<i>Scytosiphon lomentarius</i> Lyngb.		18			
<i>Scytosiphon pygmaeus</i> Reinke		1			
* <i>Sorapion simulans</i> Kuck.	X	1	Ku1894b		
<i>Sphacelaria caespitula</i> Lyngb.	X		Ku1894b	KS, H	
<i>Sphaceloderma helgoleticum</i> Kuck.					
as <i>Sphacelaria olivacea</i> (Pringsh.)		5			
<i>Sphacelaria cirrosa</i> (Roth) C. Agardh	X	1	Hal, W1881, Ku1894b	see PHR1982	
<i>Sphacelaria irregularis</i> Kütz.					
<i>Sphacelaria pennata</i> (Huds.) Lyngb.					
<i>Sphacelaria nana</i> Nägeli ex Kütz.	X		Hal, Ku1894b, Ku1897a	KS	
<i>Sphacearia furcigera</i> Kütz. var. <i>saxatilis</i> Kuck.		2			X
<i>Sphacelaria olivacea</i> Pringsh.					
<i>Sphacelaria plumigera</i> Holmes	X	4	R1891a, R1891b, R1892		
<i>Sphacelaria plumosa</i> Lyngb.	X	14	Hal, W1881, R1891a, R1891b, Ku1912, N1925	KS, Lü, H, Leu, B	X
<i>Chaetopteris plumosa</i> (Lyngb.) Kütz.					
<i>Sphacelaria plumula</i> Zanardini	X	6	Hau, W1881, R1891a, R1891b, R1892, Ku1894b		
<i>Sphacelaria racemosa</i> Grev.			Hau, see PHR1982	see PHR1982	
as <i>Sphacelaria radicans</i> (Dillwyn) C. Agardh					X
<i>Sphacelaria radicans</i> (Dillwyn) C. Agardh	X	2	W1881, R1891b, Ku1894b, Ku1905, N1925	KS, H	
<i>Sphacelaria rigidula</i> Kütz.			Ku1894b, Ku1897a, R1891a	KS	
<i>Sphacelaria furcigera</i> Kütz.					
<i>Spongonema tomentosum</i> (Huds.) Kütz.	X		Kütz, W1881, Ku1960	KS, H	X
<i>Ectocarpus tomentosus</i> (Huds.) Lyngb.		8			
<i>Spongomorpha tomentosa</i>					
* <i>Sporochnus pedunculatus</i> (Huds.) C. Agardh	X	4	Kütz, Hal, W1881, R1891a		X

Table 2 (continued)

CHLOROPHYCOTA:	Herb. Ku	No.	1845-1935	1959-1998	Herb. KS
* <i>Stictyosiphon soriferus</i> (Reinke) Rosenv.	X		Ku1912	KS	
<i>Stictyosiphon tortilis</i> (Rupr.) Reinke		16			
<i>Stragularia clavata</i> (Harv.) Hamel	X		Ku1894b		
<i>Ralfsia borneyi</i> Kütz.					
<i>Ralfsia clavata</i> (Carmich.) P. Crouan et H. Crouan		1			
<i>Streblonema fasciculatum</i> Thur. in Le Jol.			Hau, Ku1954		
* <i>Streblonema volubile</i> Pringsh.			W1881, Pr		
* <i>Striaria attenuata</i> (C. Agardh) Grev.			W1881	KS	X
<i>Stypocaulon scoparium</i> (L.) Kütz.			Hal, W1881		
<i>Spacelaria scoparioides</i>					
<i>Symphyocarpus strangulans</i> Rosenv.	X	2	Ku1894b		
<i>Tilopteris mertensii</i> (Turn.) Kütz.	X	9	R1891a, Ku1912, D1930	KS, Lü, Kuhl	X
Drift specimens in Kuckuck Herbarium:					
<i>Alaria esculenta</i> (L.) Grev.	X	1			
<i>Elachista scutulata</i> (Sm.) Duby	X	1			
<i>Sacchoriza polyschides</i> (Lightf.) Batters	X	3			
Doubtful records:					
<i>Asperococcus bullosus</i> J. V. Lamour.			W1881		
<i>Encoelium bullosum</i> (C. Agardh) J. V. Lamour.					
<i>Asperococcus compressus</i> A. W. Griffith ex Hook.			W1881		
<i>Haloglossum griffithsianum</i> Kütz.					
<i>Compsonema minutum</i> (C. Agardh) Kuck.			W1881		
<i>Ectocarpus monocarpus</i> C. Agardh					
<i>Ectocarpus fasciculatus</i> var. <i>abbreviatus</i> (Kütz.) Sauv.			W1881		
<i>Ectocarpus abbreviatus</i> Kütz.					
<i>Ectocarpus fasciculatus</i> var. <i>refractus</i> (Kütz.) Ardissonne			Kütz, W1881		
<i>Ectocarpus refractus</i>					
<i>Ectocarpus flagelliformis</i> Kütz.			W1881		
<i>Ectocarpus approximatus</i> Kütz.					
<i>Ectocarpus ceratoides</i> Kütz.					
<i>Ectocarpus parvulus</i> Kütz.			W1881		
<i>Ectocarpus rufulus</i> Kütz.			W1881		
* <i>Halothrix lumbricalis</i> (Kütz.) Reinke			W1881		
<i>Ectocarpus lumbricalis</i> Kütz.					
<i>Myriotrichia clavaeformis</i> Harv.			Hal		
<i>Sphacelaria fusca</i> (Huds.) Gray			W1881		
<i>Sphacelaria tribuloides</i> Menegh.			W1881		
RHODOPHYCOTA:					
<i>Acrochaetium daviesii</i> (Dillwyn) Nägeli	X		W1881	KS, Leu	
<i>Callithamnion lanuginosum</i>					
<i>Chantransia daviesii</i> (Dillwyn) Thuret		7			
<i>Acrochaetium secundatum</i> (Lyngb.) Nägeli	X		Hal, W1881	KS	
<i>Callithamnion daviesii</i> Lyngb.					
<i>Chantransia secundata</i> (Lyngb.) Thuret		6			
<i>Acrochaetium seirolanum</i> (Harvey - Gibson) G. Hamel	X				
<i>Rhodochorton seirolanum</i> Harvey - Gibson		1			
<i>Acrochaetium virgatulum</i> (Harv.) Batters				KS	
* <i>Aglaothamnion byssoides</i> (Arnott ex Harv. in Hook.) Boudour. et Perret-Boudouresque				KS	
<i>Callithamnion byssoides</i> Arnott ex Harv. in Hook.					
<i>Aglaothamnion hookeri</i> (Dillwyn) Maggs et Hommers.				KS, H, B	
<i>Callithamnion hookeri</i> (Dillwyn) Gray					
<i>Ahnfeltia plicata</i> (Hudson) Fries	X	9	Hal, W1881, R1891a, N1925	KS, Lü, H, B	X
<i>Gymnogrongus plicatus</i> (Huds.) Kütz.					

Table 2 (continued)

CHLOROPHYCOTA:	Herb. Ku	No.	1845-1935	1959-1998	Herb. KS
<i>Sterrocolax decipiens</i> F. Schmitz		2			
* <i>Antithamnion cruciatum</i> (C. Agardh) Nägeli	X	7	Ku1894b		Drift
<i>Antithamnionella floccosa</i> (O. F. Müll.) Whittick				KS	
* <i>Apoglossum ruscifolium</i> (Turn.) J. Agardh	X		W1881, Hau, R1891a, Ku1894b, N1925		
<i>Delesseria ruscifolia</i> (Turn.) J. V. Lamour.		9			
? <i>Hypoglossum ruscifolium</i>					
<i>Bangia atropurpurea</i> (Roth) C. Agardh	X		W1881, R1891a, N1925	KS, H, B	X
<i>Bangia crispa</i> Hornem.					
<i>Bangia fuscopurpurea</i> (Dillwyn) Lyngb.		6			
* <i>Bonnemaisonia hamifera</i> Hariot	X		N1925	KS1962a, KS, Lü, H, B	X
<i>Trailiella intricata</i> Batters		1			
<i>Brongniartella byssoides</i> (Gooden. et Woodw.) F. Schmitz	X		Kütz, W1881, N1925	KS, Lü, H, B	X
<i>Polysiphonia byssoides</i> (Gooden. et Woodw.) Grev.		14			
* <i>Callithamnion corymbosum</i> (Sm.) Lyngb.	X	15	Hal, Ku1897c, R1891a	B	
<i>Callithamnion tetricum</i> (Dillwyn) S.F. Gray	X	2			
<i>Ceramium deslongchampsii</i> Chauv. ex Duby	X	10	Kütz, W1881, Hau, R1891a, Ku1905, S1928, D1930	KS, Lü, H, B	X
<i>Ceramium strictum</i> (Kütz.) Rabenh.					
<i>Gongroceras deslongchampsii</i> (Chauvin ex Duby) Kütz.					
<i>Gongroceras strictum</i> Kütz.					
<i>Ceramium rubrum</i> C. Agardh nom. illeg.	X	39	Hal, W1881, R1891a, N1925	KS, Lü, H, B	X
<i>Ceramium lanciferum</i> Kütz.					
* <i>Chondria dasyphylla</i> (Woodw.) C. Agardh	X		Hal, W1881, Hau, R1891a, Ku1905, S1928		
<i>Laurencia dasyphylla</i> (Woodw.) Grev.		11			
<i>Chondrus crispus</i> Stackh.	X	25	Hal, W1881, R1891a, N1925	KS, Lü, H, B	X
<i>Coccotylus truncatus</i> (Pallas) M. J. Wynne et J. N. Heine	X		Hal, W1881, R1891a, N1925	KS, Lü, H, B	
<i>Actinococcus roseus</i>		4			
<i>Actinococcus subcutaneus</i> (Lyngb.) Borenv.		1			
<i>Coccotylus brodiaei</i> (Turn.) Kütz.		1			X
<i>Phyllophora brodiaei</i> (Turn.) Endl.		24			
<i>Phyllophora truncata</i> (Pallas) Zinova					
* <i>Compsothamnion gracillimum</i> De Toni	X	3	Ku1897a		
<i>Corallina officinalis</i> L.	X	15	Hal, W1881, R1891a, N1925, S1928	KS, Lü, H, B	X
<i>Cruoria pellita</i> (Lyngb.) Fries	X	7	W1881, R1891a, Ku1905, N1925	KS	
* <i>Cruoria stilla</i> Kuck.			Ku1897a		
<i>Cystoclonium purpureum</i> (Huds.) Batters	X		Hal, W1881, R1891a, N1925	KS, Lü, H, B	X
<i>Cystoclonium purpurascens</i> (Huds.) Kütz.		26			
<i>Delesseria sanguinea</i> (Huds.) J. V. Lamour.	X	21	Hal, W1881, R1891a, Ku1894b, N1925	KS, Lü, H, B	X
* <i>Dudresnaya verticillata</i> (With.) Le Jol.	X		N1925	KS	
<i>Dudresnaya coccinea</i> (C. Agardh) P. Crouan et H. Crouan		2			
<i>Dumontia contorta</i> (S. G. Gmel.) Rupr.	X		Hal, W1881, R1891a	KS, Lü, H, B	X

Table 2 (continued)

CHLOROPHYCOTA:	Herb. Ku	No.	1845-1935	1959-1998	Herb. KS
<i>Dumontia filiformis</i> Flor. dan.		13			
<i>Dumontia incrassata</i> (O.F. Müll.) J. V. Lamour.					
<i>Erythrocladia irregularis</i> Rosenv.				KS1985	
<i>Erythrodermis traillii</i> (Holmes ex Batters) Guiry et Garbary				KS, H, B	X
<i>Phyllophora traillii</i> Holmes ex Batters					
<i>Erythrotrichia carnea</i> (Dillwyn) J. Agardh			Ku1894b, N1925, S1935	KS1985	X
<i>Erythrotrichia ceramicola</i> (Lyngb.) Aresch.					
<i>Erythrotrichia reflexa</i> (P. Crouan et H. Crouan) Thur. ex De Toni				KS1985	
<i>Furcellaria lumbricalis</i> (Huds.) J. V. Lamour.	X		Hal, W1881, R1891a, Ku1905, N1925	KS, Lü, H, B	X
<i>Fastigaria furcellata</i> (L.) Stackh.					
<i>Furcellaria fastigiata</i> (Turn.) J. V. Lamour.		16			
* <i>Gelidium corneum</i> (Huds.) J. V. Lamour.			W1881		
* <i>Gloiosiphonia capillaris</i> (Huds.) Carmich. ex Berk.	X	13	Hau, R1891a	KS, Lü, Kuhl	
* <i>Gracilaria gracilis</i> (Stackh.) Steentoft, L. M. Irvine et Farnham	X		Hal, W1881, R1891a	B, Kuhl	
?as <i>Gracilaria confervoides</i> (F. H. Wigg.) Grev.					X
<i>Sphaerococcus confervoides</i> (Wiggers) Stackh.		1			
* <i>Gracilariopsis longissima</i> (S. G. Gmel.) Steentoft, L. M. Irvine et Farnh.	X		Hal, R1891a	?	
?as <i>Gracilaria confervoides</i> (F. H. Wigg.) Grev.		17			X
<i>Gymnogongrus crenulatus</i> (Turn.) J. Agardh	X		S1938a	KS, Lü, B	X
<i>Gymnogongrus norvegicus</i> (Gunnerus) J. Agardh		2			
<i>Haemescharia hennedyi</i> (Harv.) K. L. Vinogr. et T. Jacovleva	X		Hau, R1891a, N1925	KS, H	
<i>Petrocelis hennedyi</i> (Harv.) Batters					
<i>Petrocelis ruprechtii</i> Hauck		4			
<i>Halarachnion ligulatum</i> (Woodw.) Kütz.	X	16	Hal, W1881, R1891a, Ku1905, N1925, D1930	KS, Lü, B	X
<i>Harveyella mirabilis</i> (Reinsch) F. Schmitz et Reinke	X	3	Ku1894a, Ku1897a	KS	
<i>Choreocolax albus</i> Kuck.					
<i>Helminthocladia calvadosii</i> (J. V. Lamour. ex Duby) Setch.	X		Hau, R1891a	KS1980a	X
<i>Helminthocladia purpurea</i> (Chauv.) J. Agardh		14			
* <i>Helminthora divaricata</i> (C. Agardh) J. Agardh	X	10	Kütz, W1881, Hau, R1891a		
<i>Mesogloia divaricata</i> C. Agardh					
<i>Mesogloia hornemanni</i> Suhr ex Hornemann					
<i>Hildenbrandia rubra</i> (Sommerf.) Menegh.	X	3	W1881, R1891a, N1925	KS, H, B	
<i>Hildenbrandia rosea</i> Kütz.					
<i>Hildenbrandia sanguinea</i> Kütz.					
<i>Hydrolithon farinosum</i> (Lamour.) D. Penrose & Y. M. Chamb.	X				
<i>Melobesia farinosa</i> Lamour.		1			
* <i>Jania rubens</i> (L.) J. V. Lamour.	X		Hal, W1881, R1891a, Ku1905		
<i>Corallina corniculata</i> L.					
<i>Jania corniculata</i> (L.) J. V. Lamour.					
<i>Corallina rubens</i> L.		3			
<i>Jania spermophoras</i> J. V. Lamour.					
<i>Lithophyllum orbiculatum</i> (Foslie) Foslie				KS	
<i>Lithothamnion sonderi</i> Hauck	X	1	Hau, Ku1897a, Hey, Ku1905, N1925	KS, Leu	
<i>Lomentaria clavellosa</i> (Turn.) Gaillon	X		Hal, R1891a, S1928	KS, H, Lü, B	X

Table 2 (continued)

CHLOROPHYCOTA:	Herb. Ku	No.	1845-1935	1959-1998	Herb. KS
<i>Chylocladia clavellosa</i> (Turn.) Grev.		24			
<i>Lomentaria orcadensis</i> (Harv.) Collins ex W. R. Taylor	X		R1888, R1891a	KS, Lü, H, B	X
<i>Chylocladia rosea</i> Harv.		10			
* <i>Mastocarpus stellatus</i> (Stackh.) Guiry			W1881, Hau	KS, B	X
<i>Gigartina mamillosa</i> (Gooden. et Woodw.) J. Agardh					
<i>Mastocarpus mamillosus</i>					
<i>Melobesia membranacea</i> (Esper) J. V. Lamour.	X	4	W1881, Ku1894b, N1925	KS, H, Leu	X
<i>Membranoptera alata</i> (Huds.) Stackh.	X		Hal, Hau, R1891a, N1925	KS, Lü, H, B	X
<i>Delesseria alata</i> (Huds.) J. V. Lamour.		19			
* <i>Nemalion helminthoides</i> (Velley) Batters	X		Hal, W1881, Hau, R1891a	KS	
<i>Nemalion multifidum</i> (F. Weber et D. Mohr) Endl.		6			X
* <i>Osmundea ramosissima</i> Athanasiadis	X		Hal, Hau, R1891a, Ku1905, N1925, S1928		
<i>Laurencia pinnatifida</i> S. G. Gmel.		9			
<i>Peyssonnelia dubyi</i> P. Crouan et H. Crouan	X	2	W1881, Ku1897a, R1891a, Ku1905	KS	
<i>Phycodrys rubens</i> (L.) Batters	X		Kütz, Hal, W1881, Hau, Ku1894b, Ku1905, N1925	KS, Lü, H, B	X
<i>Delesseria sinuosa</i> (Gooden. et Woodw.) J. V. Lamour.		12			
<i>Phycodrys sinuosa</i>					
<i>Phyllophora crispa</i> (Huds.) P. S. Dixon	X		Hal, W1881, Hau, R1891a, Ku1905, N1925	KS, Lü	
<i>Phyllophora rubens</i> (Gooden. et Woodw.) Grev.		14			
<i>Phyllophora pseudoceratoides</i> (S. G. Gmel.) Newroth et A. R. A. Taylor	X		R1891a, Ku1905	KS, Lü, H, B	
<i>Phyllophora membranifolia</i> Endl.		19			X
<i>Phymatolithon calcareum</i> (Pallas) W. H. Adey et McKibbin			Hey, Ku1905, N1925	KS, H	
<i>Lithothamnion polymorphum</i> (L.) Aresch.					
<i>Phymatolithon polymorphum</i> (L.) Foslie					
<i>Phymatolithon laevigatum</i> (Foslie) Foslie			Ku1897a, Hey	KS, H	
<i>Lithothamnion embolooides</i> Heydrich					
<i>Lithothamnion laevigatum</i> Foslie					
<i>Phymatolithon lenormandii</i> (Aresch.) W. H. Adey			Hau, R1891a, Hey	KS, H, Leu	
<i>Litophyllum lenormandii</i> (Aresch.) Foslie					
<i>Phymatolithon purpureum</i> (P. Crouan et H. Crouan) Woelk. et L. M. Irvine				Leu	
* <i>Plagiospora gracilis</i> Kuck.			Ku1897a		
<i>Plocamium cartilagineum</i> (L.) P. S. Dixon	X		Kütz, Hal, W1881, Hau, N1925	KS, Lü, H, B	X
<i>Plocamium coccineum</i> (Huds.) Lyngb.		16			
<i>Plocamium coccineum</i> f. <i>binderianum</i>					
<i>Plumaria plumosa</i> (Huds.) O. Kuntze	X		Hal, W1881, Hau, N1925	KS, Lü, H, B	
<i>Plumaria elegans</i> (Bonnem.) F. Schmitz		15			X
<i>Ptilota plumosa</i> C. Agardh		2			
<i>Ptilota sericea</i> Harvey					
* <i>Pneophyllum fragile</i> Kützling	X				
<i>Melobesia lejolisi</i> Rosanoff		1			
* <i>Pneophyllum myriocarpum</i> (P. Crouan et H. Crouan) Y. M. Chamb.				Leu	
<i>Polyides rotundus</i> (Huds.) Gaillon	X	18	N1925	KS, Lü, H, B	X
<i>Polysiphonia elongata</i> (Huds.) A. Spreng.	X	31	Hal, W1881, R1891a	KS, Lü, H, B	X

Table 2 (continued)

CHLOROPHYCOTA:	Herb. Ku	No.	1845-1935	1959-1998	Herb. KS
<i>Polysiphonia fucoides</i> (Huds.) Grev. in Hook.	X		Hal, W1881, R1891a	KS, Lü, H, B	
<i>Polysiphonia nigrescens</i> (Huds.) Grev. ex Harv. in Hook.		25			X
<i>Polysiphonia violacea</i> (Roth) A. Spreng.		4			X
* <i>Polysiphonia lanosa</i> (L.) Tandy	X		Hal, W1881	KS, B	X
<i>Polysiphonia fastigiata</i> (Roth) Grev.		5			
<i>Polysiphonia nigra</i> (Huds.) Batters	X		W1881, Hau, R1891a, Ku1894b	KS, H, B	X
<i>Polysiphonia atrorubescens</i> (Dillwyn) Grev.		20			
<i>Polysiphonia badia</i> (Dillwyn) A. Spreng.					
<i>Polysiphonia stricta</i> (Dillwyn) Grev.	X		Kütz, Hal, W1881, R1891a, N1925	KS, Lü, H, B	
<i>Polysiphonia urceolata</i> (Lightf. ex Dillwyn) Grev.		18			X
* <i>Porphyra dioica</i> Brodie et L. M. Irvine				KS1991, KS, B	Isotype
as <i>Porphyra laciniata</i> C. Agardh					
* <i>Porphyra insolita</i> Kornmann et Sahling				KS1991, KS	Type
* <i>Porphyra leucosticta</i> Thur. in Le Jolis	X	14	Ku1897a	K1961d, KS, H, B	X
* <i>Porphyra linearis</i> Grev.				K1961e, KS1991, KS, H, B	X
* <i>Porphyra ochotensis</i> Nagai				K1961e, KS1991, KS, B	X
* <i>Porphyra purpurea</i> (Roth) C. Agardh				K1961e, KS1991, KS, H, B	Neo-Isotype
<i>Porphyra purpureo-violacea</i> (Roth) V. Krishnam.					
* <i>Porphyra umbilicalis</i> (L.) J. Agardh	X		Hal, W1881, R1891a, N1925	K1961e, KS1991, KS, H, B	X
? <i>Porphyra laciniata</i> Lightf.		12			
<i>Porphyra umbilicalis</i> (L.) Kütz.					
<i>Porphyra vulgaris</i> Kütz. nom. illeg.		1			
* <i>Porphyra spec.</i>				K1986	X
as <i>Porphyra yezoensis</i> Ueda					
<i>Porphyropsis coccinea</i> (J. Agardh ex Aresch.) Rosenv.	X		Ku1897a	KS1985, KS, Lü, B	X
<i>Porphyra coccinea</i> J. Agardh ex Aresch.		5			
<i>Porphyropsis imperfecta</i> Kornmann et Sahling				KS1985	
<i>Porphyrostomium ciliare</i> (Carmich.) M. J. Wynne				K1984, KS1985, KS	
<i>Erythropeltis discigera</i> (Berthold) F. Schmitz					
<i>Erythrotrichia discigera</i> Berthold					
<i>Erythrotrichopeltis ciliaris</i> (Carmich.) Kornmann					
<i>Pterothamnion plumula</i> (J. Ellis) Nägeli in Nägeli et C. E. Cramer	X		W1881, R1891a, N1925	KS, Lü, H, B	
<i>Antithamnion plumula</i> (J. Ellis) Thur. ex Le Jolis		12			X
<i>Callithamnion plumula</i> (J. Ellis) Lyngb.					
<i>Rhodochorton membranaceum</i> (Magnus) Hauck	X			KS, Lü, H	X
<i>Audouinella membranacea</i> (Magnus) Papenf.		7			
<i>Rhodochorton purpureum</i> (Lightf.) Rosenv.	X		W1881	KS, Lü	
<i>Callithamnion rothii</i> (Turton) Lyngbye					
<i>Rhodochorton rothii</i> (Turton) Näg.		6			
<i>Trentepohlia rothii</i> (Turton) Harvey					
<i>Rhodothamniella floridula</i> (Dillwyn) Feldmann in T. A. Chr.	X		W1881, Ku1897a, Ku1905, N1925	KS, Lü, H, B	
<i>Rhodochorton floridulum</i> (Dillwyn) Nägeli		5			X
* <i>Rhodomela confervoides</i> (Huds.) P. C. Silva	X		R1891a, N1925	KS, Lü, H, B	X
<i>Rhodomela subfusca</i> (Woodw.) C. Agardh		20			
<i>Rhodomela virgata</i> Kjellm.				KS, H, B	X
<i>Rhodophysema elegans</i> (P. Crouan et H. Crouan ex J. Agardh) P. S. Dixon	X		Ku1897b	KS, H, Leu	
<i>Rhododermis parasitica</i> Batters		4			

Table 2 (continued)

CHLOROPHYCOTA:	Herb. Ku	No.	1845-1935	1959-1998	Herb. KS
Sahlingia subintegra (Rosenv.) Kornmann				KS1985, K1989, Leu	
<i>Erythrocladia subintegra</i> Rosenv.					
<i>Erythropeltis subintegra</i> (Rosenv.) Kornmann et Sahling					
*Scinaia furcellata subsp. scandinavica (Maggs et Guiry) Athanasiadis	X		W1881, Hau, R1891a	KS1980a	
<i>Ginnania furcellata</i>					
<i>Scinaia furcellata</i> Biv.					
<i>Scinaia furcellata</i> (Turn.) J. Agardh		5			
*Spermothamnion repens (Dillwyn) Rosenv.	X		Kütz, Hal, W1881, Hau, R1891a		
<i>Callithamnion repens</i> (Dillwyn) Lyngb.					
<i>Callithamnion roseolum</i> C. Agardh					
<i>Callithamnion turneri</i> (Mertens ex Roth) C. Agardh					
<i>Spermothamnion roseolum</i> (C. Agardh) Pringsh.					
<i>Spermothamnion turneri</i> (Mertens ex Roth) Aresch.		14			
Stylonema alsidii (Zanardini) K. M. Drew				KS, H	
<i>Goniotrichum alsidii</i> (Zanardini) Howe					
Titanoderma pustulatum (J. V. Lamour.) Nägeli in Nägeli et C. E. Cramer				KS, H, Leu	
<i>Dermatolithon pustulatum</i> (J. V. Lamour.) Foslie					
*Tsengia bairdii (Farl.) K. C. Fan et Y. P. Fan	X		Ku1912	KS, Lü, Kuhl	X
<i>Platoma bairdii</i> (Farl.) Kuck.		5			
Drift specimens in Kuckuck Herbarium:					
Hypoglossum hypoglossoides (Stackh.) Collins et Harv.	X		Hal, W1881	Kuhl	
<i>Deleseria hypoglossum</i>		3			
<i>Hypoglossum woodwardii</i> Kütz.					
Naccaria wiggii (Turn.) Endl.	X	1	Hau		
Nitophyllum sp.	X	1			
Drift specimens in Kornmann & Sahling Herbarium:					
Acrosorium sp.					X
Antithamnionella ternifolia (C. Agardh) Nägeli					
<i>Antithamnionella sarniensis</i> Lyle					X
Callithamnion tetragonum (With.) Gray			W1881		X
<i>Callithamnion affine</i> Harvey					
Falkenbergia sp.					X
Monosporus pedicellatus (Sm.) Solier in Castagne					
<i>Monospora pedicellata</i> (Sm.) J. Agardh					X
Doubtful records:					
Acrochaetium minutissimum (Suhr) Nägeli			W1881		
<i>Callithamnion minutissimum</i> Suhr					
Alsidium corallinum C. Agardh			W1881		
Boergesenella fruticulosa (Wulfen) Kylin			Kütz, W1881		
<i>Polysiphonia fruticulosa</i> (Wulfen) A. Spreng.					
Botryocladia botryoides (Wulfen) Feldmann			W1881		
<i>Gastroclonium uvaria</i> Kütz.					
Ceramium diaphanum (Lightf.) Roth			Hal		
Compsothamnion thyoides (J. E. Smith) Nägeli			W1881		
<i>Callithamnion gracillimum</i> C. Agardh					
Corallina vancouveriensis Yendo			W1881		
<i>Corallina densa</i> (Collins) Doty					
Cryptopleura ramosa (Huds.) Kylin ex L. Newton			W1881		
<i>Cryptopleura lacerata</i> (S. G. Gmel.) Kütz.					
Dilsea carnosa (Schmidel) Kuntze			Kütz, Hau		

Table 2 (continued)

CHLOROPHYCOTA:	Herb. Ku	No.	1845-1935	1959-1998	Herb. KS
<i>Iridea edulis</i>					
<i>Sarcophylis edulis</i> (Stackh.) J. Agardh					
<i>Gastroclonium ovatum</i> (Huds.) Papenf.			W1881		
<i>Gastroclonium ovale</i> (Huds.) Lyngb.					
<i>Gastroclonium subarticulatum</i> (Turn.) Kütz.	X		Hau		
<i>Lomentaria ovalis</i> (Huds.) Endlicher		2			
<i>Heterospiphonia plumosa</i> (J. Ellis) Batters			Hau		
<i>Dasya coccinea</i> (Huds.) C. Agardh					
<i>Laurencia obtusa</i> var. <i>gracilis</i> (C. Agardh) Zanardini			W1881		
<i>Laurencia gelatinosa</i> J. V. Lamour.					
<i>Lithophyllum lichenoides</i> Philippi			Hau		
<i>Lobosiphonia obscura</i> (C. Agardh) Falkenberg nom. illeg.			W1881		
<i>Polysiphonia subadunca</i> Kütz.					
<i>Lomentaria articulata</i> (Huds.) Grev.			Hau		
<i>Chylocladia articulata</i> (Huds.) Grev.					
<i>Osmundea osmunda</i> (S. G. Gmel.) Nam et Maggs			W1881		
<i>Laurencia pinnatifida</i> var. <i>osmunda</i> Kütz.					
<i>Osmundea pinnatifida</i> (Huds.) Stackh.			W1881		
<i>Laurencia pinnatifida</i> (Huds.) J. V. Lamour .					
<i>Palmaria palmata</i> (L.) Kuntze			Hau, W1881		
<i>Rhodymenia palmata</i> (L.) Grev.					
<i>Pantoneura angustissima</i> (Turn.) Kylin			W1881		
<i>Hypoglossum angustissimum</i> (Turn.) Kütz.					
<i>Phyllophora sicula</i> (Kütz.) Guiry et L. M. Irvine			W1881		
<i>Phyllotylus siculus</i> Kütz.					
<i>Pneophyllum confervicolum</i> (Kütz.) Y. M. Chamb.			W1881		
<i>Hapalidium phyllactidium</i> Kütz.					
<i>Polysiphonia boldii</i> Wynne et Edwards			Hau		
<i>Polysiphonia hemisphaerica</i> Aresch.					
<i>Polysiphonia brodiaei</i> (Dillwyn) A. Spreng.			Kütz, W1881		
<i>Polysiphonia elongella</i> Harv.			W1881		
<i>Polysiphonia fibrillosa</i> (Dillwyn) A. Spreng.			W1881		
<i>Polysiphonia flocculosa</i> (C. Agardh) Kütz.			W1881		
<i>Polysiphonia subcontinua</i> (C. Agardh) J. Agardh					
<i>Polysiphonia opaca</i> (C. Agardh) Moris et De Notaris			W1881		
<i>Ptilota gunneri</i> P. C. Silva, Maggs et L. M. Irvine			W1881		
<i>Ptilota plumosa</i>					
<i>Rhodomela lycopodioides</i> (L.) C. Agardh			Kütz, Hau		
<i>Lophura lycopodioides</i>					
<i>Rhodymenia pseudopalmata</i> (J. V. Lamour.) P. C. Silva			W1881		
<i>Sphaerococcus palmetta</i> (J. V. Lamour.) C. Agardh					
<i>Spermothamnion strictum</i> (C. Agardh) Ardissonne			W1881		
<i>Callithamnion semipennatum</i> J. Agardh					
<i>Spyridia filamentosa</i> (Wulfen) Harvey			Kütz		

the flora as they were not mentioned again until Peter Kornmann and Paul-Heinz Sahling started their work. *Blidingia chadefaudii* was separated from *B. minima* and *B. subsalsa* from *B. marginata* by Kornmann and Sahling (1978) on the basis of developmental differences.

Bolbocoleon piliferum

This species was described by Pringsheim (1862) from Helgoland and is present with two herbarium sheets in

the herbarium of Kuckuck. As this species is widely distributed along the Swedish west coast (Kylin 1949) and southern Norway (Rueness et al. 1997), it may have been present all the time. Its recent occurrence on Helgoland has been described by Ellertsdóttir and Peters (1997).

Bryopsis spp.

Whether Kuckuck (1894b) and Schmidt (1935) were dealing with one or two species is not clear.

Chaetomorpha ligustica

This species was first observed at Helgoland in July 1967 in shallow tidal pools (Kornmann 1972). Since then it has become a regular member of the summer flora (May–September) of Helgoland.

Cladophora spp.

Seven species were determined by van den Hoek (1963) for Helgoland, including Kuckuck's herbarium material consisting of four species (see Table 2). Wollny (1881) mentioned two more species (*C. battersii* and *C. pellucida*) without referring to herbarium specimens or giving a thorough description.

Codium fragile

This foreign invader was first recorded for Helgoland with two attached plants in 1930 (Schmidt 1935). Since then it has been growing as a small population in the western part of the island on *Rhodothamniella floridula* ridges and on harbour walls in the subtidal zone (Kornmann and Sahling 1977).

Derbesia marina (including *Halicystis ovalis*)

This species is found very rarely in Helgoland in the sublittoral zone. In the Kuckuck herbarium there exists material of the Mediterranean species *D. neglecta* Berthold for Helgoland. Its identity remains to be proven.

Enteromorpha spp.

The eight *Enteromorpha* species listed for Helgoland need taxonomic re-investigation as more recent taxonomic investigations need to be considered (e.g. Koeman and van den Hoek 1982a,b; Koeman 1985; Blomster et al. 1998).

Entocladia viridis

Schmidt (1935) comments that this species was widely distributed on Helgoland in Bryozoans growing on *Fucus* or on *Halidrys siliquosa*. It might have been overlooked since then. For the taxonomic position of *Entocladia* see Silva et al. (1996).

Entonema tenuissimum

Wollny (1881) collected this species growing on *Flustra foliosa* in the dune area of Helgoland, but this is the only record. As Reinsch (1890) described this species from Antarctica, the identity of Wollny's material is doubtful.

Gomontia polyrhiza

Schmidt (1935) mentions this species growing on and in limestone underneath *Polysiphonia stricta*, north of the dune (Robbenbrunnen), a location only accessible by boat. The absence of any records since then may be due to this species being overlooked during recent collections.

Haloclorococcum spp.

Kornmann and Sahling (1983) described three new species of *Halochlorococcum*, two of those from Helgoland. No fixed material or herbarium specimens exist as Type material but Kornmann and Sahling refer to three photographic tables as Type material (Figs 21, 22 and 23) in their publication.

Prasiolopsis ramosa

This is a freshwater alga according to Christensen (1994). It grows together with *Rosenvingiella polyrhiza* and *Prasiola* spp. on harbour constructions and was found regularly in cultures of *R. polyrhiza* (Kornmann and Sahling 1974).

Rosenvingiella constricta

The third record in the North Atlantic and the first record for Helgoland of this species was in 1973 (Kornmann and Sahling 1977). The identity with North-Pacific material is not proven. It is rare in Helgoland.

Ulothrix spp.

Wollny (1881), Kuckuck (1894b) and Nienburg (1925) mention *Ulothrix flacca* (Dillwyn) Thuret for Helgoland. Kuckuck (1894b) also lists *Ulothrix collabens* (C. Agardh) Thuret. This species might be identical with *Urospora collabens* (C. Agardh) Holmes et Batters. Burrows (1991) recognizes *Ulothrix flacca* as a separate species following Lokhorst (1978), who identified herbarium material from Helgoland from Kornmann and Sahling and from the 19th century as *U. flacca*. Kornmann (1964a), however, regarded *U. flacca* as a synonym for *U. speciosa*. Kornmann (1964a: 31) described *Ulothrix flexuosa* as a new species. According to Lokhorst (1978) this is an invalid name as *U. flexuosa* was used by Schussnig (1915) for a separate taxon. *U. flexuosa* Kornmann, however, is a synonym for *U. speciosa* (Carmich. ex Harv. in Hooker) Kütz. (Lokhorst 1978). There exist many permanent microscope slides of this species on Helgoland.

Ulva spp.

Several species of *Ulva* have been described for Helgoland. It has not been established with certainty that *U. kuckuckiana* (Schmidt 1935), which was separated from a plant considered to be *U. latissima* f. *nana* by Kuckuck (1894b), is identical with *U. curvata* (Kornmann and Sahling 1977). Plants formerly described as *U. curvata* (Kornmann and Sahling 1977) were referred to *U. pseudocurvata* (Kornmann and Sahling 1994) due to the missing hollow stipe and the marginal wings with small cells in the rhizoidal area of the thallus (see Koeman and van den Hoek 1981). According to Kornmann and Sahling (1994) there is no *U. lactuca* on Helgoland as the *Ulva* populations there do not exhibit a stiff thallus, a characteristic that separates *U. lactuca* from the thinner *U. pseudocurvata*. However, a recent morphological investigation of *Ulva* spp. (Kuhlenkamp, unpublished) provides evidence that most of the eulittoral and sublittoral *Ulva* plants belong to *U. lactuca* and only a limited population in the northeastern harbour to *U. pseudocurvata*. The recently described species *U. tenera*, which has only been recorded from Helgoland and Sylt (Kornmann and Sahling 1994), is an unusual form of *Ulva*, growing in the upper eulittoral and propagating with zoospores with only two flagella. Its relationship to *U. linearis* from Morocco (Dangeard 1957) and *U. neapolitana* from the Mediterranean (Bliding 1960, 1968) remains to be elucidated (Kornmann and Sahling 1994). The Type of *U. tenera* is present at the Marine Biological Station on Helgoland.

Phaeophycota

Ascophyllum nodosum

Many old records for Helgoland may refer to drift material that is regularly washed up on the island. However, a few specimens in the herbarium of Kuckuck were lettered as attached plants from the western part of the island. After 1959 a small population was established in the protected south harbour and this is currently in a state of expansion (Bartsch and Wagner, personal observation).

Arthrocladia villosa

This species was always rare on Helgoland with only one herbarium sheet, probably from the late 19th century: Wollny (1881) mentioned a herbarium specimen of Gätke collected in the 1870s which is probably the same one that Reinke (1891a) refers to. Kuckuck (1894b) described another specimen that developed in culture attached to a stone dredged in December 1893 from 10–15 m depth. In the Netherlands *Arthrocladia* is absent (Stegenga et al. 1997), and in Scandinavia it is only a rare deep-water species often occurring together with

Sporochnus pedunculatus. Recently, a few individuals were found at 61°N in Norway at a depth of 18–22 m thereby extending the northern boundary of the species (Lein 1996). In Danish waters it has only rarely been observed in recent years (Nielsen 1998). Due to its deep-water occurrence on gravel and sand, it may have been overlooked.

Asperococcus fistulosus

Kuckuck (1905, 1912) described this species as growing at the northern part of Helgoland in summer, but there is no subsequent record. This species is generally considered rare in the Netherlands (Stegenga and Mol 1983), in Kent (SE England; Tittley and Price 1977) and on the Swedish west coast (Kylin 1947). Nielsen et al. (1996) considered it extinct for the German and Danish Wadden Sea area. In Norway, however, it is recorded along the whole coastline (Rueness et al. 1997).

Chilionema reptans

This may be a stage in the life history of *Asperococcus fistulosus* (Pedersen 1984).

Cladostephus spongiosus

In the Kuckuck herbarium both forms of *C. spongiosus* (Huds.) C. Ag., *forma spongiosus* and *forma verticillatus* (Lightf.) Prud'homme van Reine were determined and confirmed by Prud'homme van Reine personally.

Compsonema saxicola

This is probably a stage in the life cycle of *Scytosiphon* or *Petalonia* (Fletcher 1987).

Corynophlaea crispa

At the turn of the century this species was commonly found on *Chondrus crispus* during May/June at Nordhornbrunnen or dune reefs (Kuckuck 1929); however, there have been no records since then. There are no recent records from the Netherlands, Denmark and Norway (Nielsen et al. 1995; Rueness et al. 1997; Stegenga et al. 1997).

Cutleria multifida

Wollny (1881) mentioned collections of *Cutleria* plants from 3–5 m depth in the Nordhafen area, together with *Aglaozonia* crusts, but considered them as rare. Twenty years later the crusts of *Aglaozonia parvula* were still

one of the more frequent species on Helgoland and were found at all times of the year, but the gametophyte *Cutleria multifida* was very rare (Kuckuck 1894b, 1900). The *Aglaozonia* stage was recorded up to 1925 (Nienburg 1925). The species is still present in southern Norway (Rueness et al. 1997) while the gametophyte is rarely found in the Danish Kattegatt (Nielsen 1998). From the Netherlands the species is only reported as drift (Stegenga et al. 1997) and in SE England it is also very rare (Tittley and Price 1977).

Delamarea attenuata

There is only a single record of this high arctic species in Helgoland (Kuckuck 1894b) with two herbarium sheets from the Kuckuck collection that need confirmation.

Dictyosiphon foeniculaceus

This species was a common member of the Helgoland flora from the middle of the 19th century up to the late 1960s (Hallier 1863; Kornmann and Sahling 1977), but has not been recorded since then. It mainly grows on *Chordaria flagelliformis* and has its main occurrence in July (Kuckuck 1912). Along the Danish Baltic sea coast and in Norway it is a frequent species (Nielsen et al. 1995; Rueness 1977).

Dictyota dichotoma

The earliest collection of this species was that of Sonder who first found *Dictyota dichotoma* in Helgoland in 1854 (Cohn 1865). In the 1860s it was found abundantly in the very shallow subtidal zone in the west of the island (Hallier 1863; Cohn 1865). Since then it has become a conspicuous member of the littoral zone up to the beginning of the 1960s. Kornmann's last herbarium specimens from the littoral zone are dated November 1961 and November 1962 (Kornmann and Sahling 1994). This species is now no longer found in its original habitat. There was a single sublittoral finding in 1969 (Lüning 1970). Since 1989, however, this species has again been found regularly in the form of a few individuals in the southern harbour and in a sheltered basin west of that harbour (Kornmann and Sahling 1994). In summer 1999 there was even a thick meadow growing in the shallow subtidal of the sheltered basin. Whether the formerly littoral and the recent sublittoral forms belong to the same genetic entity is unknown.

Ectocarpus lucifugus

This species was newly described by Kuckuck (1897b) from Helgoland. Kuckuck pointed out the distinctness of *E. lucifugus* and *Leptonema lucifugum* (see *Pilinia*

rimosa) in cell width, form and amount of chromatophores per cell and formation of unilocular versus plurilocular zoidangia. Hooper et al. (1987) confirm that *E. lucifugus* is a distinct entity from *Pilinia rimosa* after examining Type material (in Herb. BM). Two herbarium sheets are still present on Helgoland.

Eudesme virescens

Kuckuck described this species as a summer entity for Helgoland just appearing in August (Kuckuck 1929) with seven herbarium records between July 1893 and August 1905. Later records of this species for Helgoland do not exist. In the Netherlands it is only known as drift (Stegenga et al. 1997), but in the Danish Baltic and along the whole Norwegian coastline it is a frequent species (Nielsen et al. 1995; Rueness et al. 1997).

Fucus ceranoides

This estuarine species was described as new for Helgoland by Kornmann and Sahling (1994). It is characterized by its distinctly elongated air bladders that differ from *F. spiralis* and *F. vesiculosus*. On Helgoland these plants grow atypically in a fully marine environment and not in the freshwater-influenced sites that are the preferred habitat of this species. The representative morphology of *F. ceranoides* is not present in Helgoland. Kornmann suspected that it represented a hybrid because some plants also bore vesicles as in *F. vesiculosus*. Unusual air bladders at the tips may be present in other *Fucus* species on Helgoland as well, especially in *Fucus spiralis*, and probably represent morphological variation or a disease. Comparison with material of *F. ceranoides* from England does not show similarities to the Helgoland specimens. On the other hand, the fan-shaped receptacles without a rim as shown in Kornmann and Sahling (1994: 391) are unusual for *F. spiralis*. A recent morphological investigation of Helgoland *Fucus* species (Munda and Kremer 1997) unfortunately does not comment on *F. ceranoides* but strengthens the point that Helgoland *Fucus* populations are longer and significantly narrower than *Fucus* specimens from other western European sites.

Hecatonema terminale

This entity may be a stage in the life history of some Punctariaceae (Fletcher 1987). Kuckuck (1897a) collected it from chalk stones but not from *Fucus vesiculosus* as observed by Kützing (1845).

Himanthalia elongata

Drift material is found regularly on Helgoland (Kornmann and Sahling 1994). Recently a small attached pop-

ulation of the button-like sporophytes without receptacles was found in the same sheltered basin west of the south harbour together with *Dictyota dichotoma* (Kuhlenkamp, personal observation), but not in the south harbour itself. As there were only few individuals present no herbarium specimens were made.

Hincksia fuscata

In the herbarium of Kuckuck one specimen labelled as *Ectocarpus fuscatus* Zanardini by Kuckuck was considered to be the Type material of *Hincksia fuscata* var. *uber* Kuckuck (collected 7 May 1900) by Kornmann.

Isthmoplea sphaerophora

The first record for the German marine flora was that of Reinke (1892) on Helgoland. It is found in the sublittoral, growing epiphytically on red algae, especially *Polysiphonia stricta* (Reinke 1892; Kornmann and Sahling 1977).

Kuetzingiella maculans

This species was described as *Ectocarpus* (?) *maculans* Kuck. and is not identical with *Ectocarpus maculans* P. A. Dang. that was transferred to *Streblonema maculans* (P. A. Dang.) South & Tittley. It was found growing in thin irregular, yellowish brown spots on *Phymatolithon calcareum* at 6–10 m depth from August to October (Kuckuck 1956).

Leathesia difformis

This was a typical summer species for Helgoland at the beginning of the 20th century at Nathurn cliffs in the northeast and in the western part of the island, growing from June to September mainly on *Chondrus crispus* or *Corallina officinalis* (Schmidt 1928; Kuckuck 1929). Damman (1930) mentioned that the species was still found in 1925 on the western part of the island but it disappeared after the installation of breakwaters. Herbarium records between May 1862 and August 1905 are present. In July 1999, a small population of *L. difformis* in the western part of the island that is seldom visited by collectors was rediscovered by I. Tittley. The specimens had unilocular and plurilocular zoidangia present on the same thalli. This species is found in the Netherlands, the Danish Baltic, and along the whole Norwegian coastline, but is rare in SE England (Tittley and Price 1977; Nielsen et al. 1995; Rueness et al. 1997; Stegenga et al. 1997).

Mesogloia vermiculata

This species was listed several times during the 19th century (Hallier 1863; Reinke 1891a), but was never

found by Kuckuck on Helgoland between 1892 and 1918 (Kuckuck 1929). Nevertheless three herbarium records from August 1905 are present.

Mikrosyphar polysiphoniae

In the herbarium of Kuckuck there is a note that permanent microscopic slides exist of this species that might have represented Type material. However, all the permanent slides made by Kuckuck have been destroyed.

Petalonia filiformis

This species has been reported once for Helgoland in the winters of 1894/95 and 1895/96 by Kuckuck (1897a), and one herbarium sheet is available. Otherwise this species only rarely occurs on the southeastern and eastern shores of England and Scotland (Fletcher 1987).

Pilinia rimosa

This species was described for Helgoland as *Leptonema lucifugum* by Kuckuck (1897b) and was later transferred to *Waerniella lucifuga* (Kuck.) Kylin (Kylin 1947). Investigations by Hooper et al. (1987) confirmed morphological identity between *W. lucifuga* and *Pilinia rimosa* with the name of *P. rimosa* having precedence. Silva et al. (1996: 717) discussed the troubled taxonomic history of the genus *Pilinia*. Although the original habitat of the marine caverns was lost, Tittley (1982) mentioned *W. lucifuga* for vertical red sandstone cliffs in the western part of the island and A.F. Peters collected it in 1987 on the western side (Lummenfelsen) and established an unialgal culture (Peters, personal communication).

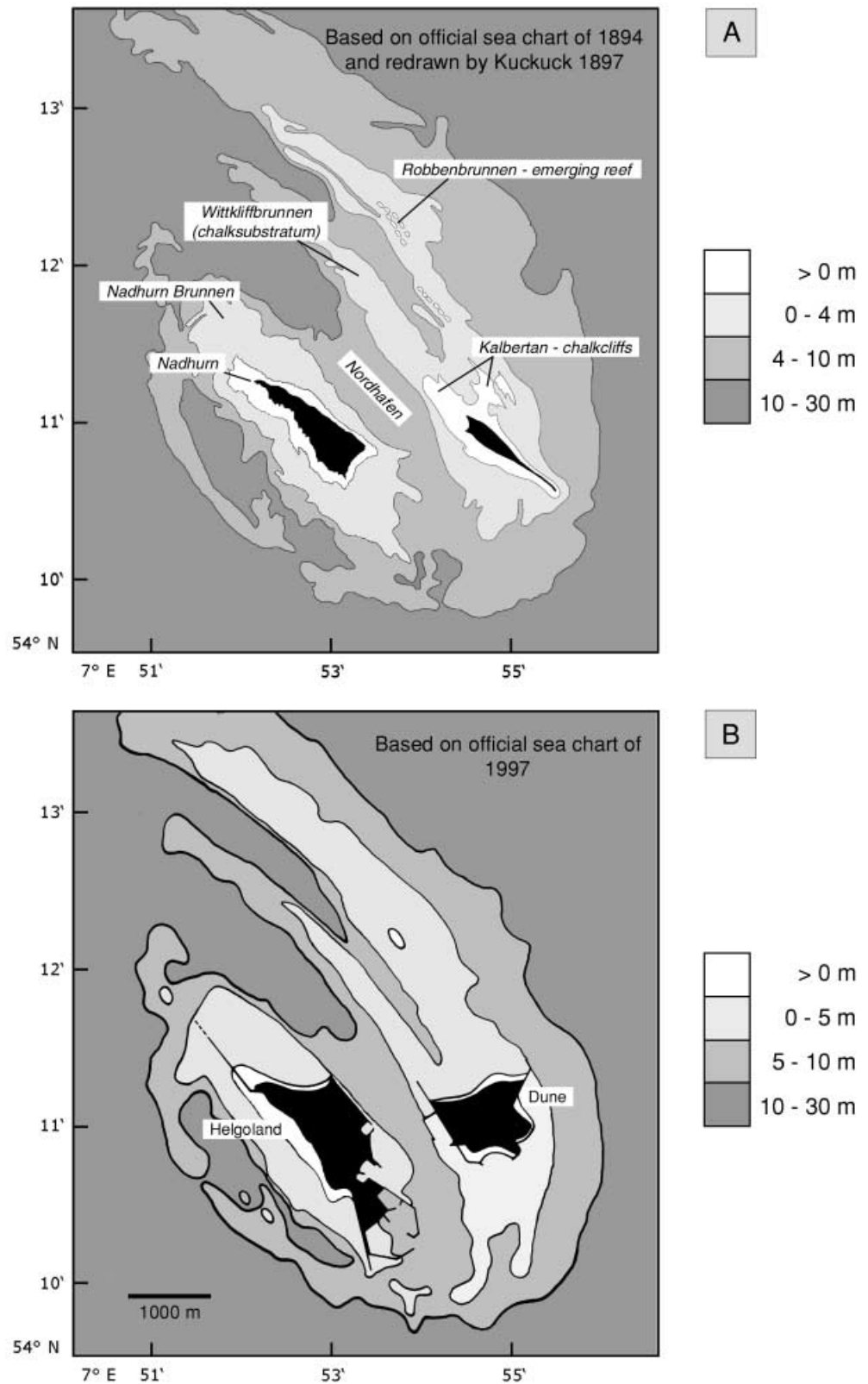
Sargassum muticum

Attached plants were first recorded in 1988 in the southern harbour of Helgoland. This species is increasingly common in summer since 1990 and grows at different shallow subtidal sites around the island (Kornmann and Sahling 1994; Bartsch, personal observation).

Sauvageaugloia griffithsiana

At the beginning of the 20th century this was a common species in summer from the beginning of August to the end of September on shallow pebbles at the NE part of the dune (Kalbertan), according to Kuckuck (1912) but not documented by herbarium specimens. This habitat was later destroyed by expanding the dune area (Fig. 1). There are also no recent records from Norway (Rueness et al. 1997), Denmark (Nielsen et al. 1995) and the Netherlands (Stegenga et al. 1997).

Fig. 1 Sea charts of the area around Helgoland (North Sea) with depth contours in metres below MLSW at the end of the 19th century (**A**) and the end of the 20th century (**B**). Distinct changes of the outlines of the main island and the “Dune” area are apparent, especially the loss of large intertidal areas in the north of both islands. **A** is based on the original drawing of Kuckuck (1897a) including the names of the locations given by him. **B** was redrawn from the official nautical chart of 1997



Sorapion simulans

This is a rare species of unknown distribution. It is a small sublittoral brown crust described by Kuckuck (1894b) for Helgoland where it grew together with *Pseu-*

dolithoderma extensum at a depth of 5–10 m; there have been no further records for Helgoland since. Only a single specimen has been reported for the British Isles (southern England) (Fletcher 1987), and there are no records for the Netherlands, Denmark and Norway

(Nielsen et al. 1995; Rueness et al. 1997; Stegenga et al. 1997).

Sporochnus pedunculatus

This was a rare deep-water species. Reinke (1891a) first mentioned it for Helgoland and referred to the herbarium at Kiel. On Helgoland there are four herbarium specimens, two from 1868 (Gätke's herbarium) and two drift specimens collected by Kuckuck in August 1897. Since then there have been no further records for Helgoland. There are also no records for the Netherlands, and only local findings in the Danish Skagerrak and some places in southern Norway (Nielsen et al. 1995; Lein 1996; Rueness et al. 1997; Stegenga et al. 1997). It could be that all Helgoland records were drift.

Stictyosiphon soriferus

This species was collected on Helgoland from March to August at the beginning of the 20th century (Kuckuck 1912). After 1950 it was only recorded three times between 1952 and 1960 (Kornmann and Sahling 1977).

Streblonema volubile

This species was described by Pringsheim (1862) for Helgoland and mentioned by Wollny (1881) who cited Pringsheim (1862) but obviously did not collect it himself.

Striaria attenuata

This species was only collected once in July 1971 in a deep artificial basin west of the south harbour (Kornmann and Sahling 1977) and Wollny (1881) refers to a specimen in the herbarium of Gätke, but did not collect it himself. This species has also been absent from the Netherlands for almost 150 years, but has recently re-established in Lake Grevelingen (Otten and Prud'homme van Reine 1992). It is present in the northern Baltic and south-western Norway (Nielsen et al. 1995; Rueness et al. 1997).

Rhodophycota

Aglaothamnion byssoides

It cannot be established whether the recorded plants belong to *Aglaothamnion* or *Callithamnion* as nuclei per cell were not determined (see Kornmann and Sahling 1983; Maggs and Hommersand 1993).

Antithamnion cruciatum

There are many specimens in the herbarium Kuckuck collected between 1893 and 1900. There is the possibility that it was confused with *Spermothamnion* species (Maggs and Hommersand 1993).

Apoglossum ruscifolium

According to Kuckuck (1897c) individuals of this species only appeared in summer within a short period of 4–6 weeks during which the plants germinated, became fertile and died; there were no further records after 1925. This species is still present in southern Norway and the Danish Kattegat (Nielsen et al. 1995). In Denmark the species is found growing on pebbles in regions that also exhibit a steep temperature gradient between 0 and 18°C similar to Helgoland (Nielsen, personal communication). Hardy (1998) reports that this species disappeared at the beginning of the 20th century from the coastlines of NE England (Northumberland and Durham).

Bonnemaisonia hamifera

The filamentous *Trailiella*-phase of this species has been common in the subtidal zone throughout the year since the 19th century. Gametophytic *Bonnemaisonia* plants were first recorded after 1959 and are only present infrequently after relatively warm autumn and winter conditions. Very large populations were present in 1968 and 1969 (Kornmann and Sahling 1977). Between 1996 and 1998 a few drift gametophytes were found each summer. In June and July 1999 many fertile plants of both sexes were found in deeper channels of the NE littoral zone (herbarium specimens present).

Callithamnion corymbosum

This species is a summer annual according to Kuckuck (1897c) that was frequently collected in the 19th century near the low water level (Hallier 1863). There are no records between 1900 and 1995. In July 1999, specimens found growing epiphytically on *Ceramium rubrum* attached to floating pontoons in the southern harbour were identified by Ian Tittley. This species has long been confused with *Aglaothamnion byssoides* due to its very sparse cortication near the base and because no nuclear staining was carried out (see Maggs and Hommersand 1993). In 1995, specimens believed to be *Aglaothamnion byssoides* were isolated into culture by A. Wagner and were recently identified as *Callithamnion corymbosum* after nuclear staining by I. Bartsch and A. Wagner. This species is frequent in the Danish Baltic and southern Norway, but very rare and perhaps extinct in the German part of the Wadden Sea (Nielsen et al. 1995; Rueness et al. 1997; Schories et al. 1997).

Chondria dasyphylla

This species was always infrequent on Helgoland (Hallier 1863). In the herbarium of Kuckuck there are more than 13 specimens collected in August or September between 1894 and 1905, but the species was recorded up to 1925 on the western part of the island in tidal pools together with *Laurencia pinnatifida* and *Corallina officinalis* (Nienburg 1925; Schmidt 1928); there have been no records since.

Compsothamnion gracillimum

Male specimens were found in 1894 and 1896 on limestone (Kuckuck 1897a). The morphology of the spermatangia differs from other populations, but it is possible that the formation of sterile tips on the spermatangial heads is an anomaly that requires further study (Maggs, personal communication). There are no further records since Kuckuck.

Cruoria stilla

This is probably the crust of *Halarachnion ligulatum* (Maggs and Guiry 1989).

Dudresnaya verticillata

This is a very rare species on Helgoland. In Kuckuck's herbarium there are three undated sheets and one specimen from 16 August 1905 without a location. After 1959 there is only one record, in August 1972 (Kornmann and Sahling 1977).

Gelidium corneum

This species is only mentioned once by Wollny (1881) and he refers to a herbarium specimen of Gätke without a note questioning whether it might be drift.

Gloiosiphonia capillaris

This is a rare summer deep-water species with only five records after 1959, but 13 herbarium sheets from the end of the 19th century. The most recent records were in 1975 (drift material; Sahling, personal communication) and in 1997 when a large population was observed in shallow water north of the dune (Kuhlenkamp, personal observation).

Gracilaria/Gracilariopsis

In the 19th century and again from the late 1980s onwards, specimens referable to these genera were collect-

ed in the subtidal zone of Helgoland. Material in the herbarium Kuckuck under the name of *Gracilaria confervoides* (Kuckuck 14.7.1896) is *Gracilariopsis longissima* and material collected recently (1.7.1998 by R. Kuhlenkamp) is *Gracilaria gracilis* as was determined by M. Steentoft (for further detail see Steentoft et al. 1995; Steentoft and Farnham 1997). Whether both species are present on Helgoland today is unknown. On the Wadden Sea island of Sylt, *Gracilariopsis longissima* and *Gracilaria gracilis* (both under the name of *Gracilaria verrucosa*) have become increasingly rare in recent years, but were still abundant in the 1950s (Schories et al. 1997).

Helminthora divaricata

There are ten herbarium sheets in the herbarium of Kuckuck, found during July and August between 1877 and 1905. There have been no other reports.

Jania rubens

This species was only recorded up to 1905 in Helgoland; simultaneously this species disappeared from Denmark, the Netherlands and SE England (Tittley and Scott 1998). The most recent record for Denmark was 1927 (Nielsen 1998). Rodriguez-Prieto and Polo (1996) observed a negative effect of pollution on the biomass of *Jania rubens* in the NW Mediterranean. Best growth is only achieved under reduced phosphorus conditions (von Stosch 1969), indicating a susceptibility to eutrophic waters.

Mastocarpus stellatus

The first record of attached plants was in 1983 on basaltic rocks in the western part of the island (Kornmann and Sahling 1994). Within 16 years this species had become very prominent on all man-made and natural hard substrata around the island; it is also present on soft red sandstone and still is extending its area. It forms extensive stands especially on exposed sites along the southwestern moles. The spreading of this species has substantially changed the appearance of some of the intertidal biotopes during recent years. The two records of Wollny (1881) and Hauck (1885) for Helgoland are considered doubtful, as this well-defined intertidal species should have been noticed by Kuckuck and later phycologists if it had been present.

Nemalion helminthoides

Hallier (1863) described this species as frequent for Helgoland. It was also listed by other workers (Hauck 1885; Wollny 1881; Reinke 1891a) and is present in the Kuckuck herbarium. Subsequently the species became

very rare. Neither Schmidt nor Nienburg mentioned it for the 1920s and 1930s and Kornmann only found two specimens in September 1959 (Kornmann and Sahling 1977). There have been no records since.

Osmundea ramosissima

Maggs and Hommersand (1993) reported *Laurencia truncata* Kützing from Helgoland, which was recently transferred to *O. ramosissima* (Nam et al. 2000). Their decision was based on two specimens in the herbarium at Lund, one undated and probably collected by Binder, the other by David Hylmö in July 1922, both with a discoid base and secondary pit connections. In the Kuckuck herbarium, specimens listed under the name of *Laurencia pinnatifida* with discernible holdfasts have discoid bases and thus may also belong to *Osmundea ramosissima*. However, further comparisons of this material with other *Osmundea* species is required. The last record of this species was in the 1930s on the Nathurn cliffs in the northeastern part of the island (Kornmann and Sahling 1994).

Plagiospora gracilis

The genus and species were described by Kuckuck (1897a) from Helgoland on the basis of a single finding in winter 1895/96. There does not exist any other record for Helgoland, but it is also reported from Norway, the Baltic Sea and Ireland (Morton 1994; Nielsen et al. 1995; Rueness et al. 1997).

Pneophyllum spp

Pneophyllum myriocarpum was determined by Y. Chamberlain but *P. fragile* is an unverified record and was only listed once.

Polysiphonia lanosa

This epiphyte on fucoids was most probably not present on Helgoland before 1990. The records from the 19th century (Hallier 1863; Wollny 1881) do not distinguish whether they were drift or attached specimens. In the herbarium of Kuckuck most specimens were on *Ascophyllum nodosum* and labelled as drift material. Also Kuckuck's herbarium specimens of attached *Ascophyllum nodosum* do not show any sign of *P. lanosa*. Kornmann and Sahling (1994) mention that drift specimens of *Ascophyllum nodosum* often bore the epiphyte *P. lanosa*. A constant population of this species on *Ascophyllum* has only been present since the 1990s and is currently in a state of expansion (Kornmann and Sahling 1994; Bartsch, personal observation).

Porphyra spp.

Eight species of *Porphyra* have been reported from Helgoland. The specimens reported as *P. laciniata* (Kornmann and Sahling 1991) were referred to *P. dioica* by Brodie and Irvine (1997). *P. ochotensis* is a doubtful entity and isozyme electrophoresis data suggest that it may be the same as *P. dioica* (Bartsch, unpublished). *P. insolita* (Kornmann and Sahling 1991) is a separate species according to Rubisco spacer sequences (Brodie et al. 1998), but is particularly difficult to identify in the field as it is similar to *P. umbilicalis*. *P. yezoensis sensu* Kornmann was described for Helgoland on the basis of culture studies (Kornmann 1986), but is not the same as Japanese material of *P. yezoensis* according to Rubisco spacer sequence data (Brodie et al. 1998) and not the same as *P. insolita*. Before 1939 only *P. leucosticta* and *P. umbilicalis* (as *P. laciniata*) were considered to occur on Helgoland, probably due to taxonomic difficulties. The small high littoral winter species *P. linearis* is confirmed by herbarium specimens from 1956 onwards. Its distinctness from *P. hiemalis* remains to be proven (Guiry, personal communication) but it is the same as British material (Brodie et al. 1998). The report of a sublittoral epiphytic *P. linearis* in July 1923 (Schiller 1928) almost certainly refers to *Porphyropsis coccinea*.

Scinaia furcellata

This species occurred frequently in Helgoland until the beginning of the 20th century. It is documented by herbarium specimens collected in July and August between 1893 and 1905. Its upright gametophytes have not been found since. The species, however, is still found on Helgoland: Kornmann and Sahling (1980a) were able to culture upright gametophytes from shell-boring microthalli collected in May 1976 from a depth of 6 m. Maggs and Guiry (1982) separated the Helgoland, Danish and Swedish material from material found elsewhere in Europe, giving it the status of a subspecies *scandinavica*. A striking feature of the Scandinavian material is the pointed apices in contrast with the rounded apices of north-west European material. Herbarium material of Kuckuck in most cases shows pointed apices and thus fits into ssp. *scandinavica*.

Spermothamnion repens

This species was regularly recorded in the 19th century (e.g. Kützing 1845; Hallier 1863; Wollny 1881). There are no further records since Kuckuck's herbarium specimens, which were collected between 1893 and 1905.

Tsengia bairdii

This species is rare in Helgoland, but was already recorded by Kuckuck between August 1897 and 1907.

There are occasional records between 1959 and 1982 with the latest finding of tetrasporangial plants being in August 1997 north of Dune.

Discussion and conclusions

The island of Helgoland is an oasis for the marine phyto-benthos in the German Bight and the whole south-eastern North Sea, as it is surrounded by large stretches of sandy and muddy bottoms without any macroalgal vegetation (Reinke 1888). The flora of Helgoland comprises 274 species in total, a relatively small number in comparison with the surrounding cold-temperate coastlines of Britain and Ireland, France and Scandinavia. A species directory for the British Isles and surrounding seas includes 820 macroalgal species (Guiry 1997), while for the northern part of the Kattegat about 325 species are listed and for the Norwegian coastline 370 macroalgal species (Nielsen et al. 1995; Rueness et al. 1997). The coastal flora of NE England, which is also surrounded by long stretches of sandy coastlines, is composed of about 270 species, comparable to the number of macroalgae in Helgoland, and in the Netherlands with its soft bottomed coastline 230 species have been recorded (Hardy 1998; Stegenga and Prud'homme van Reine 1998).

In comparing the species lists available for the 19th and 20th centuries, clear differences between the beginning and the end of the 20th century are apparent. Even more differences are apparent when compared to the first check list compiled by Wollny (1881), possibly due to nomenclatural and taxonomic problems. Various factors are responsible for the situation. The detection of species may depend on their life histories, on the quantity, location and time period of sampling, on the change of natural habitats and environmental triggers such as temperature and nutrients, and on the invasion of species. Finally the individual areas of taxonomic expertise of different scientists also generate a skewed picture of the floristic composition, and taxonomic and nomenclatural problems add to this. The contribution of such factors to the observable changes in species composition in Helgoland will be discussed in detail later.

Type of life histories

It has become clear that most of the species with a life cycle comprising perennial or pseudoperennial macroscopic stages have consistently been recorded over the last 150 years and represent a stable marine flora. Exceptions are *Chondria dasyphylla*, *Jania rubens* and *Osmundea ramosissima*. It is assumed that these species are especially sensitive to a changing environment, although the critical factors are not known. *Jania rubens*, for example, disappeared simultaneously from several shores around Europe at the beginning of the century (Tittley and Scott 1998) indicating that this might be an especially sensitive indicator organism for changes in eutrophication levels.

Interestingly, most of the species that had always been rare or became rare or presumably extinct in Helgoland are species with a heteromorphic life history exhibiting annual or seasonal macroscopic stages and mostly perennial microscopic stages. Furthermore, it is obvious that species with their main appearance in summer or spring were especially likely to disappear from Helgoland or to be recorded only rarely. These include: *Apoglossum ruscifolium* (summer, in August, Kuckuck 1894a), *Asperococcus fistulosus* (summer, epiphytic), *Arthrocladia villosa* (summer on small stones, gravel, shells), *Bonne-maisonia hamifera* (summer), *Cutleria multifida* (probably annual) and its *Aglaozonia stage* (perennial), *Dictyosiphon foeniculaceus* (spring and summer), *Dictyota dichotoma* (spring and summer), *Dudresnaya verticillata* (summer on pebbles), *Eudesme virescens* (spring to summer), *Gloiosiphonia capillaris* (summer), *Helminthocladia calvadosii* (summer), *Helminthora divaricata* (summer on gravel, shells), *Leathesia difformis* (spring and summer), *Mesogloia vermiculata* (summer), *Sauvageaugloia griffithsiana* (August/September), *Sporochnus pedunculatus* (spring and summer), *Stictyosiphon soriferus* (spring and summer), *Striaria attenuata* (summer), *Scinaia furcellata* (summer on pebbles) and *Tsengia bairdii* (summer). Some of these species are sublittoral forms and therefore might be under-recorded due to insufficient collection. It is assumed that some of these species may be used as indicator organisms for environmental change.

Species with a type of life history that includes a clear winter to spring maximum, however, have been regularly recorded over the last few decades (e.g. *Monostroma* spp., *Scytosiphon lomentaria*, *Petalonia* spp., *Dumontia contorta* and *Porphyra linearis*). This suggests that some of the summer annuals need specific conditions in spring or winter that are only encountered on Helgoland intermittently, or may have not occurred for a long time. The rediscovery of *Leathesia difformis* in 1999 after more than 60 years, as well as the culturing of *Helminthocladia calvadosii* and *Scinaia furcellata* from sublittoral microthalli (Kornmann and Sahling 1980a) is, however, an indication that the hardier of the heteromorphic phases of many rare or supposedly lost species still exist in Helgoland.

Species with isomorphic or heteromorphic life histories comprising only microscopic or crustose stages, such as many endophytic or epiphytic species, can only be assessed by using culture studies and specialized and often rare taxonomic expertise. These species are very difficult to identify in the field and a positive or negative record is unsuitable as a basis for a long-term prediction. Examples are the increased records of microscopic green algae after 1959 due to Peter Kornmann's research activities and the many records of small brown algae of the Ectocarpales *sensu lato* studied by Paul Kuckuck at the end of the 19th century or the newly recorded endophytic brown algal species (Peters and Ellertsdóttir 1996; Burkhardt and Peters 1998).

Change of substratum

Species that require a special substratum also contributed to a changing species composition. The natural substrata on Helgoland are red sandstone, chalk and flint stone. The building of protective moles, harbour constructions and breakwaters from the early 1920s onwards created diverse new habitats on new substrata (wood, concrete, basalt, granite, steel) enabling many species to colonize the island or to enlarge their area. It is probable that the broad establishment of many Chlorophyta such as *Blidingia* spp., *Prasiola* spp. or *Rosenvingiella* spp. as well as of some red algae of the genus *Porphyra* and *Mastocarpus stellatus* was favoured by artificial hard substrata. However, these taxa (except *Mastocarpus*) may have been present before in small unrecorded quantities.

The erection of protective moles also destroyed some habitats such as the marine caves at the western part of the island, inhabiting *Pilinia rimosa* and *Ectocarpus lucifugus*.

The expansion of the dune area destroyed a substantial part of the littoral and sublittoral chalk cliffs (compare Fig. 1A with Fig. 1B), a habitat for some of the rare summer red algae such as *Gloiosiphonia capillaris*, *Helminthocladia calvadosii*, *Scinaia furcellata* and *Tsengia bairdii* or the summer brown alga *Sauvageaugloia griffithsiana*. Furthermore, the enlargement of the dune sand-covered part of the Nordhafen area (Fig. 1A) that was traditionally a pebble region. The reduction of this habitat may have contributed to the loss of *Apoglossum ruscifolium*, a species that is encountered on pebbles in the Danish Baltic (Nielsen, personal communication). The *Aglaozonia* stage of *Cutleria multifida* has also been collected there.

Introduced species

Some changes in species composition took place because of the introduction of foreign species. These include *Bonnemaisonia hamifera* and its *Trailliella* phase, *Codium fragile*, *Mastocarpus stellatus* and *Sargassum muticum*. The first two species have either a restricted habitat or occur only infrequently while *Mastocarpus stellatus* and *Sargassum muticum* altered the appearance of some biotopes drastically with their massive growth and continued expansion around the island.

Other species common on British or French shores also arrived at Helgoland and established new populations, partly creating new biotopes. *Ascophyllum nodosum*, which first colonized the protected harbour walls, has since colonized many areas with protected hard substrata around the island. Originally the *Ascophyllum* population on Helgoland was free of its epiphyte *Polydora lanosa*. This species subsequently arrived as well (in the 1990s) and is currently in a state of expansion. *Chaetomorpha ligustica* arrived only in the 1960s and since then large populations have been found during

the summer in shallow channels at the northeastern part. The newly recorded *Porphyra* species such as *P. dioica* (= *Porphyra laciniata* in Kornmann and Sahling 1991) or *P. insolita* represent a taxonomic problem and probably have been confused with other species. Drifting algal material may be a good vector for new introductions. In 1999 many drifting *Himanthalia elongata* plants around Helgoland were covered at their bases with a carpet of species common in Brittany and southern England (Kuhlenkamp and Wagner, unpublished observations). Table 2 gives an account of species that have been collected as drift on Helgoland.

Abiotic factors

Temperature

Abiotic factors such as nutrients and temperature have varied over the considered time period and might have also contributed to change. Since exact autecophysiological knowledge of most rare or supposedly extinct species is missing, it is difficult to draw conclusions. Daily surface water temperature data for Helgoland have been taken since 1872 with the exception of the two World Wars. For this time period extrapolated data exist (Becker et al. 1997). Between 1875 and 1897 there were ten winters (January–March) with mean monthly surface water temperatures below 2 or even 1°C. During this time period, the summer temperatures were unusually high with temperatures greater than 17°C in August in 13 of the years. This means that the temperature gradient was rather steep during these years. Nevertheless all of the species considered lost were recorded for Helgoland. For example, Nienburg (1925) recorded the intertidal warm-temperate *Dictyota dichotoma* in 1922 even after a very cold winter with periods of frost in the littoral. Then, between 1898 and 1939, only five winters with similarly low mean surface water temperatures occurred. Furthermore the 1930s had been a decade with especially warm summer temperatures (Becker et al. 1997). This means that the first decades of the 20th century had been relatively warm. The 1940s had been a decade with four extremely cold winters, three of them in succession (mean temperatures in February and March below 0°C). This was exceptional for the whole time period since 1872 and could have caused the extinction of warm-temperate species like *Corynophlaea crispa* or *Cutleria multifida*. Then the temperature gradient between summer and winter became more moderate again. Only in the 1990s did a similarly warm decade as in the 1930s occur (Franke et al. 1999) with mean winter temperatures between 3°C and 6.5°C and mean summer temperatures between 17.35°C and 18.48°C (Becker et al. 1997).

The spatially restricted sublittoral recurrence of *Dictyota dichotoma* since 1989 may thus be a reintroduction favoured by the elevated winter temperatures in Helgoland in the 1990s compared to the 1980s (Franke et al. 1999). As a positive indicator for relatively warm

autumn and winter temperatures, the massive occurrence of *Bonnemaisonia hamifera* during the following summer may be used, as the induction of tetraspores in its *Trailliella* phase is restricted to temperatures above 11°C and a critical daylength of 12 h (Breeman and Guiry 1989).

Nutrients

There is a daily time series of nutrient analysis from Helgoland Road from 1962 onwards showing an increase in nitrate and phosphate content of the seawater (Hickel et al. 1997). During the 1960s the phosphorus content of the seawater at Helgoland nearly doubled up to 0.9 µmol/l, and only fell again from the mid-1980s onwards. The nitrate eutrophication was different. Up to 1979 the yearly mean of nitrate concentration in the seawater was below 10 µmol/l. Then it rose drastically with a peak value of 30 µmol/l in 1987. From 1980 onwards the mean summer concentration for nitrate never fell below 4 µmol/l at Helgoland (Hickel et al. 1997). Experimental evidence is lacking to prove any influence of the changed nutrient conditions on the disappearance of most of the above mentioned species except for *Jania rubens* (von Stosch 1969) and *Nemalion helminthoides* (Cunningham and Guiry 1986).

Conclusions

One hypothesis to explain the described changes in species composition is that the species considered have very special demands regarding photoperiod, temperature and perhaps nutrients in order to become reproductive or to grow; in other words they may have a narrow reproductive window allowing the microphase to produce the macrophase. Generally, species with small reproductive windows are especially sensitive to slight seasonal changes as seen in the gametophytes of *Nemalion helminthoides* which are summer annuals. The induction of erect axes from the prostrate filaments is optimal at daylengths between 14 h and 16 h and temperatures between 7°C and 13°C. The induction time is about 4 weeks (Cunningham and Guiry 1989 for Irish isolates from more or less the same latitude as Helgoland). The induction of tetrasporangia needs about 2 weeks and takes place at short daylengths of less than 12 h and within a temperature range of 10–18°C. Tetrasporophytic and gametophytic microthalli may reproduce vegetatively by monospores under a wide range of conditions (van den Hoek 1982). Generally these characteristics make it possible for *N. helminthoides* to grow in Helgoland although the openings in the reproductive windows are narrow. There are about 6–8 weeks in May and June with a daylength of >14 h and temperatures of >7 and <13°C for the induction of gametophytes, and about the same time in October/November with daylengths of <12 h and temperatures of < 18 and > 10°C for the induction of tetra-

spores (see Lüning 1990, p. 313, for the annual oscillation of daylength in Helgoland). A slight change toward lower temperatures in spring or higher temperatures in autumn may close the apparent window. Furthermore, higher turbidity of the water due, for example, to increased plankton blooms certainly alter the daylength under water. Possible induction times at Galway are similarly short and there *N. helminthoides* is a regularly occurring species (for temperature and annual oscillation of daylength at Galway see Breeman and Guiry 1989). Additionally, Cunningham and Guiry (1986) also report a nutritional effect in *Nemalion helminthoides*. Optimum erect axis development and optimal tetrasporangium formation took place only at reduced nitrate and phosphate levels in the culture medium; very low nitrate levels, however, inhibited tetrasporangial formation. The elevated nitrate and phosphate levels at Helgoland due to eutrophication in the second half of the 20th century (Hickel et al. 1997) should therefore be considered as one regulator of the recruitment of *N. helminthoides* in Helgoland.

This study illustrates that the evaluation of species composition over time has its limitations when attributing long-term changes to specific environmental or physiological factors. A thorough knowledge of the role of abiotic factors in determining the growth and reproduction of sensitive species can help to explain changes in species composition. A future task will be to identify marine indicator species for the various types of environmental changes expected, such as in temperature, irradiance, sea level changes or nutrient concentrations.

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